DIEL AND DEPTH VARIATIONS IN THE SEX-SPECIFIC ABUNDANCE, SIZE COMPOSITION, AND FOOD HABITS OF QUEENFISH, *SERIPHUS POLITUS* (SCIAENIDAE)

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ABSTRACT

Lampara seine-hauls were taken during day and night over 5-27 m bottom depths off the coast of northern San Diego County, California, from September 1979 to March 1981. These samples were used to characterize the temporal and spatial patterns of the abundances and size and sex compositions of queenfish, *Seriphus politus*, in an unprotected, coastal environment. Stomach contents of sample queenfish were examined to aid our interpretation of these patterns.

Adult queenfish of both sexes made diel, onshore, and offshore migrations, but immature fish generally did not. Both immatures and adults occurred in epibenthic, resting schools in shallow areas (~10 m or less depth, within ~1.5 km of shore) during the day. At night, adult fish dispersed (to >3.5 km) offshore. On average, a greater fraction of the adult males emigrated farther offshore at night than adult females. Immature fish remained inshore of 16 m bottom depths (within ~2.5 km of shore) at night, with the majority staying inshore of ~10 m depth. Regardless of maturity class, larger fish occurred farther offshore at night.

Stomach contents data confirmed the primarily nocturnal feeding habits of both immature and adult queenfish. Immatures fed primarily on meroplankton and other nearshore prey; however, adults captured offshore had also eaten some nearshore prey. Thus, food habits explain much, but not all of the diel migratory pattern. Immature queenfish may also remain nearshore at night because migration is not worthwhile energetically and because of greater risk of predation offshore. Adults perhaps also migrate offshore at dusk to spawn.

Numerous physical and biological factors influence the spatial and temporal distribution patterns of fishes. In response to such factors, coastal marine fishes often undergo diel shifts in spatial distributions (reviewed by Woodhead 1966; Blaxter 1970). Examples of horizontal (Hobson 1965, 1973; Hobson and Chess 1976; Quinn et al. 1980; Allen and DeMartini 1983) and vertical or water-column (Parrish et al. 1964; Woodhead 1964; Beamish 1966) diel migrations are recognized. Diel horizontal migrations may vary with life stage (e.g., see Hobson and Chess 1973). The type of diel vertical movement also may vary with season and with age and spawning condition of fish (Hickling 1933; Lucas 1936; Brawn 1960; Blaxter and Parrish 1965; Beamish 1966). In other cases, relatively static differences between the depth distributions of juvenile and adult life stages have

been documented (reviewed by Helfman 1978). Spatial segregation of adult males and females has been commonly observed only in tropical reef fishes (Moyer and Yogo 1982; Clavijo 1983; and others).

This study describes the manner in which a complex interplay of the factors listed above can determine the temporal and spatial patterns of the distribution of a temperate marine fish. Specifically, we report on diel shifts in the onshore, offshore distribution of queenfish, *Seriphus politus*, characterize the variation in these diel shifts for immature, adult male, and adult female fish, and relate these shifts to feeding, antipredator, and breeding functions previously described.

The queenfish is a small, schooling sciaenid whose center of geographic distribution lies in the Southern California Bight, south of Point Conception (Miller and Lea 1972). The species contributes significantly to the sport fish catch on piers in southern California (Frey 1971) and provides forage for several game fishes (Young 1963; Feder et al. 1974). Queenfish form inactive, epibenthic schools nearshore (at ~10 m or less bottom depth)

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during the day (Hobson and Chess 1976; Allen and DeMartini 1983). Queenfish are dispersed throughout the water column and also occur farther offshore (to 20-30 m depths) at night, where they feed (Hobson and Chess 1976; Hobson et al. 1981; Allen and DeMartini 1983) and perhaps spawn (DeMartini and Fountain 1981).

This study represents part of an ongoing environmental impact assessment of the fishes of coastal waters off San Onofre Nuclear Generating Station near Oceanside, Calif., using the queenfish as a target species. Recognition of potentially complex patterns of spatial and temporal distribution has general applicability for the design and interpretation of analogous monitoring studies and for other assessments of nearshore fish stocks (June 1972).

METHODS AND MATERIALS

Sampling Design

Catches made by lampara seines (a type of semipursing, roundhaul net, Scofield 1951) were used to characterize the distribution and abundance of queenfish in terms of catch per unit effort (CPUE), where a standard-area seine-haul was defined as the unit of effort (Allen and DeMartini 1983). All queenfish present in each seine-haul were counted aboard ship. Seines fished from sea surface to seabed over bottom depths from 5 to 27 m. For diel comparisons, a total of 14 pairs of "day" (1-6 h after sunrise) and "night" (1-6 h after sunset) cruises were made during the period from September 1979 to March 1981, inclusive. On each cruise, 1 or 2 seine-hauls were made within randomly selected subareas within each of three depth blocks (shallow, 5-10 m, 0.5-1.5 km offshore; middepth, 11-16 m, 1.5-2.5 km offshore; deep, 18-27 m, 2.5-3.5 km offshore) at each of two longshore locations, about 5 and 22 km upcoast of Oceanside, Calif. Two replicate hauls were made at each longshore location in the shallow depth block (wherein catches were most variable) on day cruises, and the two catch values averaged. For a chart of the study area and further details of gear and sampling designs, see Allen and DeMartini (1983).

CPUE and Size-Composition Data

A maximum of two subsamples of ~50 individuals each of queenfish of all sizes were randomly selected from each seine-haul and placed on ice aboard ship. In the laboratory, all fish in the subsamples were sexed macroscopically (DeMartini and Fountain 1981) into immatures (of both sexes), adult males, adult females, and sex indeterminable. (Fish of indeterminable sex comprised <5% of total catch.) Fish were measured to the nearest millimeter standard length (SL) and grouped into 5 mm length classes for analysis. For seine-hauls in which the total number of queenfish caught exceeded the total number measured, the numbers of fish of each maturity and sex category caught were estimated from the respective number measured, standardized to the total number of queenfish caught. In these cases, the length frequencies of the fishes in each sex category measured were then weighted by the estimated number of that category present in the haul.

Queenfish length-frequency data were compared between diel periods and depth blocks by Kolmogorov-Smirnov Two-Sample test (Siegel 1956). A nonparametric 3-way ANOVA (Wilson 1956), available in the IMSL Library's[3] statistical package, was used to simultaneously evaluate the effects of diel period, depth block, sampling date (cruise), and their potential interactions on the numerical CPUE of immature, adult male, and adult female fish. In all ANOVA analyses, catches made within the same depth block at the two longshore locations on a given cruise were considered separate estimates, as differences between locations were sometimes evident.

Food Habits

Additional subsamples of one queenfish per 10 mm SL length class were randomly selected from seine-hauls for analysis of food habits. Fish were examined from a larger series of 11 day and 23 night cruises (that included 8 of the aforementioned 14 paired, day/night cruises) conducted during September 1979-October 1980. These subsampled fish were placed in 10% Formalin[4] immediately following capture, after their abdominal walls had been slit to accelerate preservation. Stomachs were dissected and placed in 70% ethyl alcohol after about 1 wk of fixation. Contents of stomachs were scored for state of digestion on a scale of 0 (undigested) to 10 (prey present but totally indistinguishable). All prey were identified to lowest taxonomic category, their numbers tal-

lied, and reconstructed wet weight biomass estimated (to the nearest milligram, based on a key of reference prey weights). Values were summed for the aggregate of each taxon in each stomach. A compound measure of numbers (N), weight (Wt), and frequency occurrence (FO) of prey (IRI = {(%N + % Wt) %FO}; Pinkas et al. 1971) was used to characterize temporal and spatial variations in the overall importance of various prey to the diet of immature and adult male and female queenfish.

RESULTS

Catch per Unit of Effort

A large majority of the adults of both sexes, as well as immature queenfish, occurred at shallow depths (5-10 m) during daylight hours throughout most of the year (Fig. 1). A plurality of immature and adult fish of both sexes occurred at shallow depths at night as well; however, the distribution of numbers spread farther offshore at night, especially for adult fish (Fig. 1). The nocturnal offshore distribution appears to have been especially marked for adult males (Fig. 1B). This diel shift in the depth distribution of queenfish is characterized by the diel-by-depth interaction term in the ANOVA (Table 1). The (nearly) significant date effect for adults (and insignificant date effect for

immatures) in the ANOVA (Table 1) reflects the general offshore emigration of adult, but not immature, queenfish during late fall and early

TABLE 1.—Results of Wilson's Three-Way Nonparametric ANOVA with equal replication (Wilson 1956) for the effects of diel period (day, night), bottom depth (5-10, 11-16, 18-27 m), and date (cruise) on the lampara seine CPUE of immature, adult male, and adult female queenfish. Data for 14 paired, day/night cruises made during the period from September 1979 to March 1981, inclusive. (* denotes significance at $P \leq 0.05$).

| Maturity/ sex category	Factor	χ^2	df	P
Immatures	Diel	27.5	1	<0.001*
	Depth	52.0	2	<0.001*
	Date	10.0	13	0.69
	Diel x Depth	9.3	2	0.01*
	Diel x Date	7.8	13	0.86
	Depth x Date	14.0	26	0.97
	D x D x D	11.3	26	0.99
Adult males	Diel	34.4	1	<0.001*
	Depth	38.9	2	<0.001*
	Date	19.9	13	0.10
	Diel x Depth	5.2	2	0.08
	Diel x Date	5.6	13	0.96
	Depth x Date	13.1	26	0.98
	D x D x D	14.8	26	0.96
Adult females	Diel	50.6	1	<0.001*
	Depth	16.1	2	<0.001*
	Date	30.0	13	0.005*
	Diel x Depth	14.0	2	0.001*
	Diel x Date	7.0	13	0.90
	Depth x Date	11.4	26	0.99
	D x D x D	10.8	26	1.00
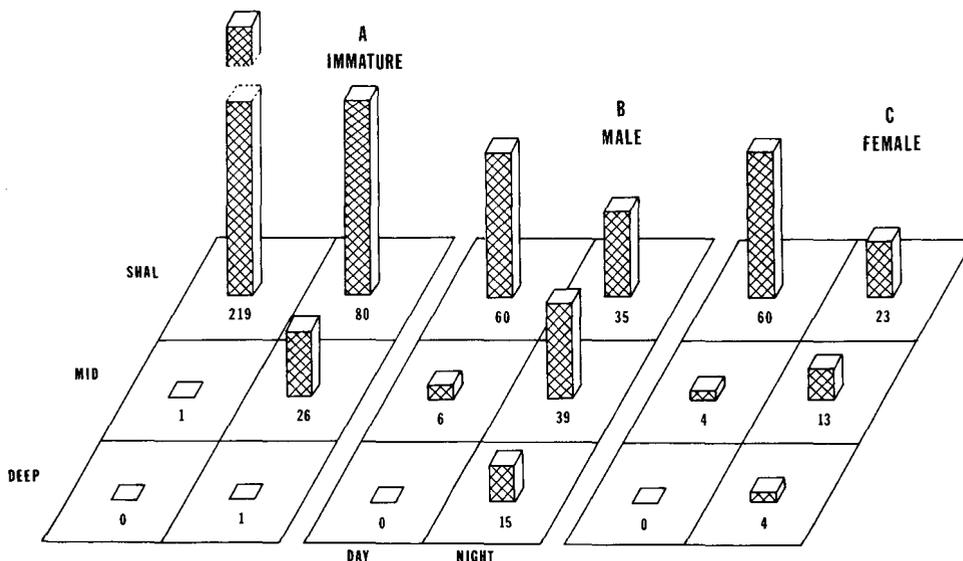
FIGURE 1.—Bar histogram chart of arithmetic mean CPUE (catch per seine haul) during the day versus at night, in the shallow (SHAL, 5-10 m), middepth (MID, 11-16 m), and deep (DEEP, 18-27 m) depth blocks, for immature, adult male, and adult female queenfish. All data represent samples from 14 paired, day/night cruises made from September 1979 to March 1981, inclusive.

winter (also see Allen and DeMartini 1983). The patterns illustrated by Figure 1 remained consistent throughout most of the year, when queenfish occurred nearshore (also see below).

Size Composition

The size composition of queenfish within sex and maturity classes also generally differed between diel periods within depth blocks (Fig. 2, Table 2). Adult males, adult females, and immature fish of both sexes were of generally larger body sizes in day versus night samples within the shallow depth block (Fig. 2, Table 2). At night, larger sized queenfish of all categories occurred in samples from middepths versus the shallow region (Fig. 3, Table 2).

The diel differences in the size composition of queenfish within depth blocks generally disappeared when catches were pooled over depth blocks throughout the year (Fig. 4). Specifically, the length-frequency distribution of each sex category in day-shallow samples closely resem-

bled the size distribution of the respective category caught at night at 5-27 m depths (Fig. 4A, B, C), even though the large numbers of fish measured (hence great power) yielded statistically significant differences (Table 2). Clearly, queenfish present at 5-27 m depths at night occur at 5-10

TABLE 2.—Results of Kolmogorov-Smirnov Two Sample comparisons (Siegel 1956) of the length-frequency distributions of sample queenfish of various sex and maturity classes between diel periods and/or depth blocks. Based on all 14 D/N pairs of cruise data for the period September 1979-March 1981. See Figures 2-4 for data histograms.

Comparison	D_{max}	D_{crit} 0.05	Significance level
Day vs. night, shallow depths			
Immatures	0.10	0.03	$P < 0.001$
Adult males	0.28	0.05	$P < 0.001$
Adult females	0.22	0.06	$P < 0.001$
Shallow vs. mid-depths, at night			
Immatures	0.26	0.06	$P < 0.001$
Adult males	0.24	0.06	$P < 0.001$
Adult females	0.12	0.09	$0.01 > P > 0.001$
Day-shallow vs. night-all depths			
Immatures	0.03	0.03	$P \sim 0.05$
Adult males	0.11	0.03	$P < 0.001$
Adult females	0.14	0.04	$P < 0.001$

IMMATURE QUEENFISH
SIZE FREQUENCIES
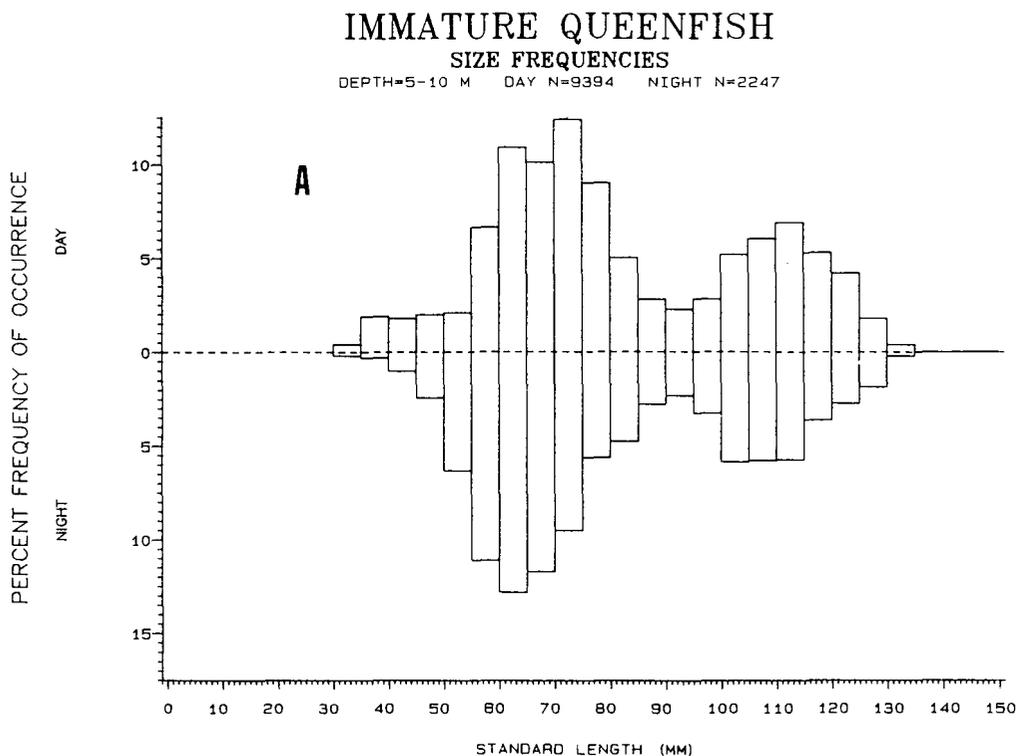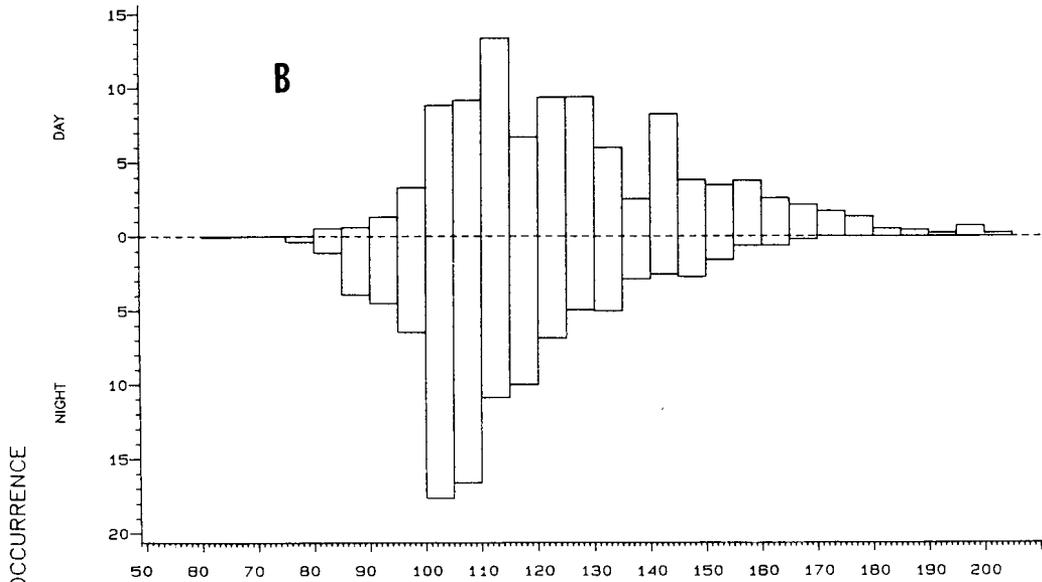DEPTH=5-10 M   DAY N=9394   NIGHT N=2247

FIGURE 2.—Relative (percent) length-frequency distributions of (A) immature, (B) adult male, and (C) adult female queenfish, caught during the day versus at night in the shallow depth block (see Figure 1 caption for details). Day/night data are plotted above, below the horizontal axis in each panel.
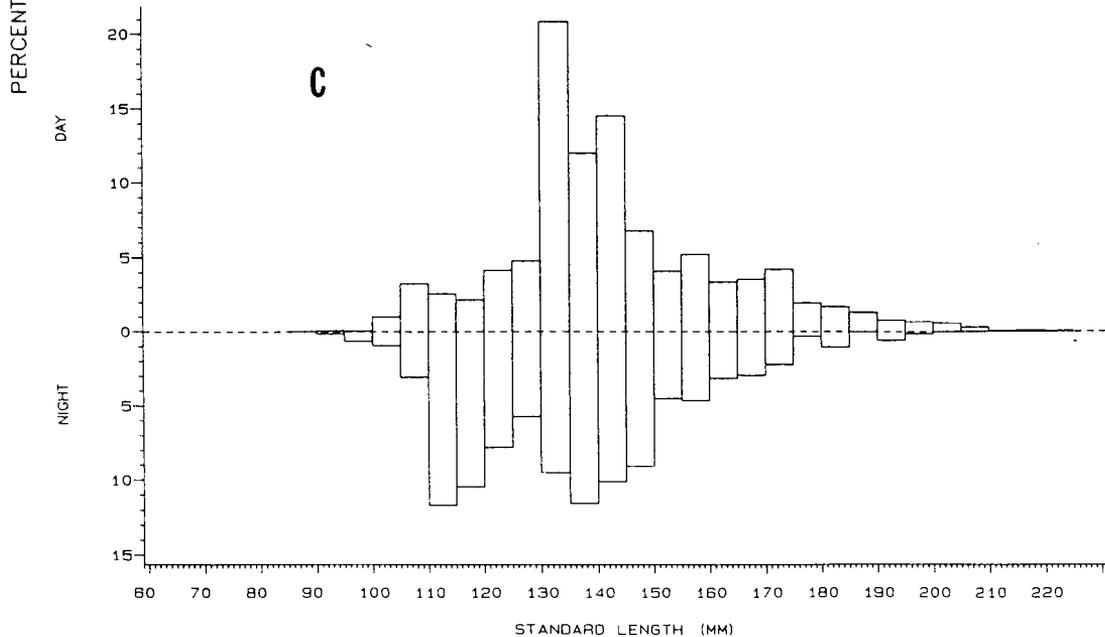
ADULT MALE QUEENFISH
SIZE FREQUENCIES
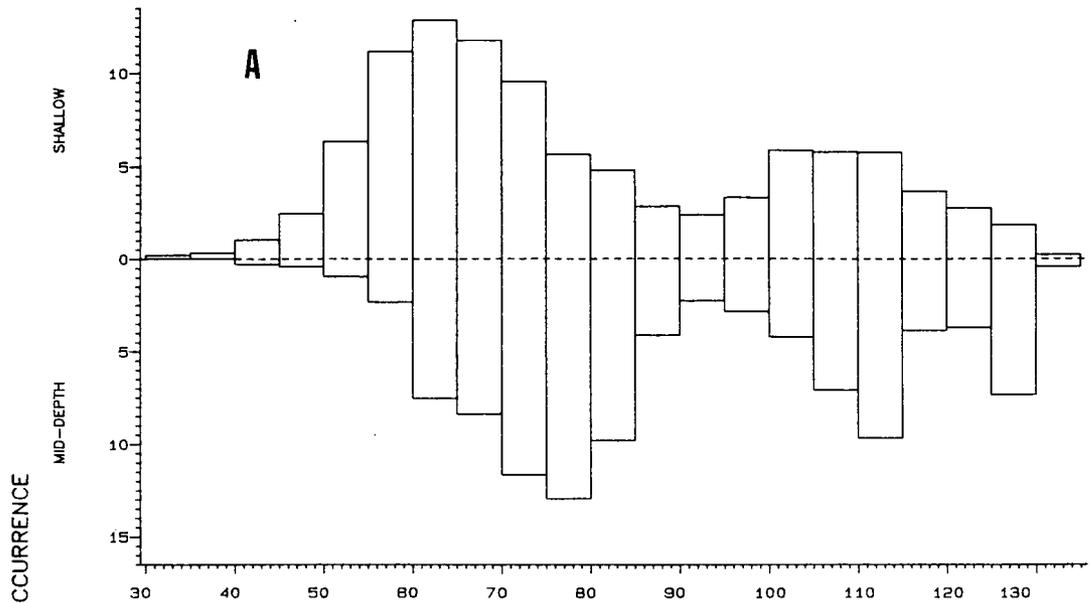DEPTH=5-10 M   DAY N=3238   NIGHT N=984

ADULT FEMALE QUEENFISH
SIZE FREQUENCIES
DEPTH=5-10 M   DAY N=3292   NIGHT N=642

STANDARD LENGTH (MM)

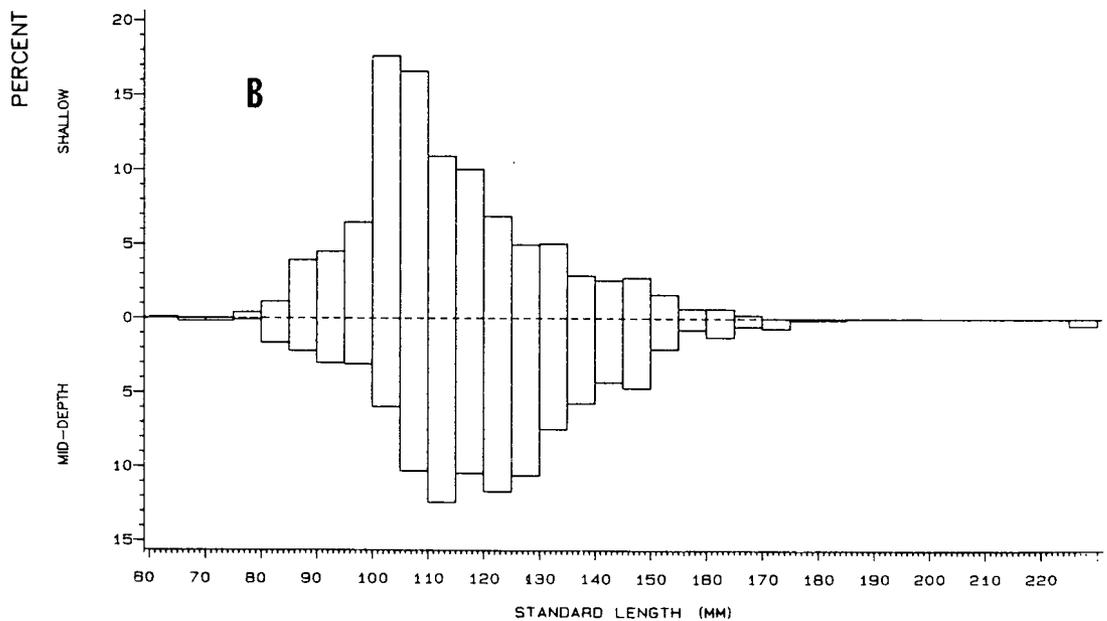PERCENT FREQUENCY OF OCCURRENCE

175

IMMATURE QUEENFISH
SIZE FREQUENCIES
NIGHT 5-10M DEPTH N=2247   NIGHT 11-16M DEPTH N=725

ADULT MALE QUEENFISH
SIZE FREQUENCIES
NIGHT 5-10M DEPTH N=984   NIGHT 11-16M DEPTH N=1096

STANDARD LENGTH (MM)

PERCENT FREQUENCY OF OCCURRENCE

ADULT FEMALE QUEENFISH
SIZE FREQUENCIES
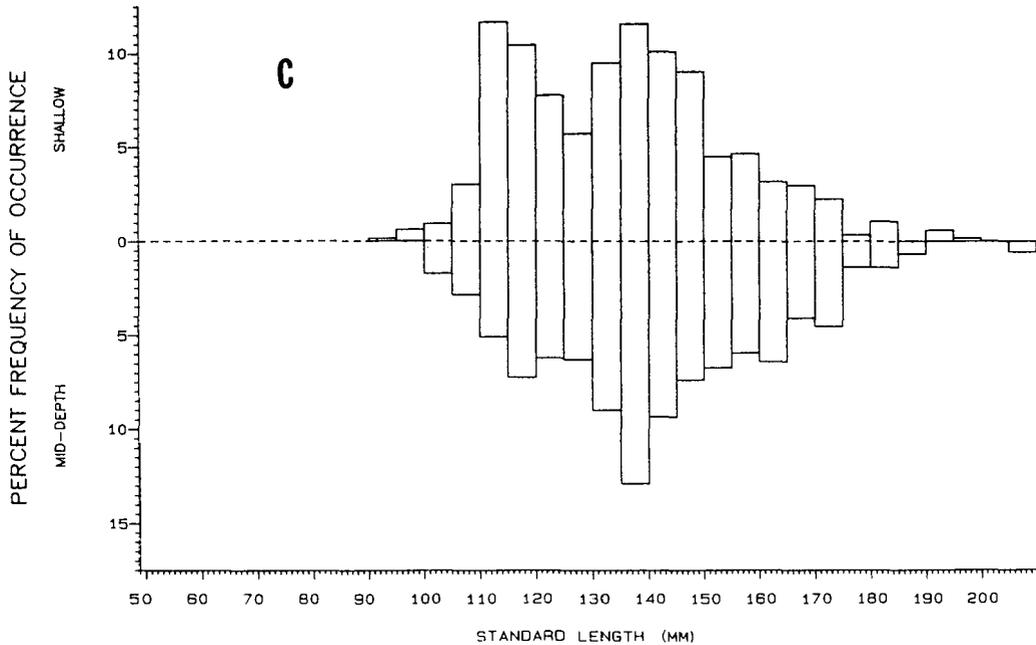NIGHT 5-10M DEPTH N=642   NIGHT 11-16M DEPTH N=350

FIGURE 3.—Relative length-frequency distributions of (A) immature, (B) adult male, and (C) adult female queenfish caught during the night in the shallow versus middepth blocks (see Figure 1 caption for details). (Data for the deep depth block were too few to evaluate independently.)

m depths nearshore during the day (also see Discussion and Conclusions).

In order to further aid our interpretation of the function of the observed nocturnal offshore movements, we subdivided our diel catch data into three periods of year: 1) February-July (the onshore, breeding season; see DeMartini and Fountain 1981); 2) August-October (the onshore, nonbreeding season); and 3) November-January (the offshore, nonbreeding season). Analyses were restricted to size-frequency data for queenfish seined at shallow and middepths during the two periods of onshore distribution, as scant data on the size composition of adults were available for the offshore season. During both breeding and nonbreeding onshore periods, queenfish seined at shallow depths were larger during the day versus at night, and fish caught at night were consistently larger in middepth versus shallow collections (Table 3). Thus the year-round patterns illustrated by Figures 2 and 3 also basically characterize both breeding and nonbreeding periods of onshore distribution.

Food Habits

The food habits of immature, adult male, and adult female queenfish were evaluated for day and night collections made in the shallow- and middepth blocks during the onshore, breeding and onshore, nonbreeding periods of year. (Stomachs of fish from the deep depth block were not examined.) The purpose of these comparisons was to help interpret the relative importance of the feeding and breeding functions of diel offshore movements. We hypothesized that immature fish might remain onshore at night to feed on meroplanktonic (nocturnally active) demersal crustaceans and other prey more abundant at shallow depths. We further expected that adults emigrated offshore to spawn (DeMartini and Fountain 1981) and thereafter fed on relatimely larger prey that were more prevalent farther offshore. In general, immature queenfish fed on smaller prey than adult males, and adult males, being smaller than adult females, fed on generally smaller prey than females (Table 4). Contrary to expectations, adult
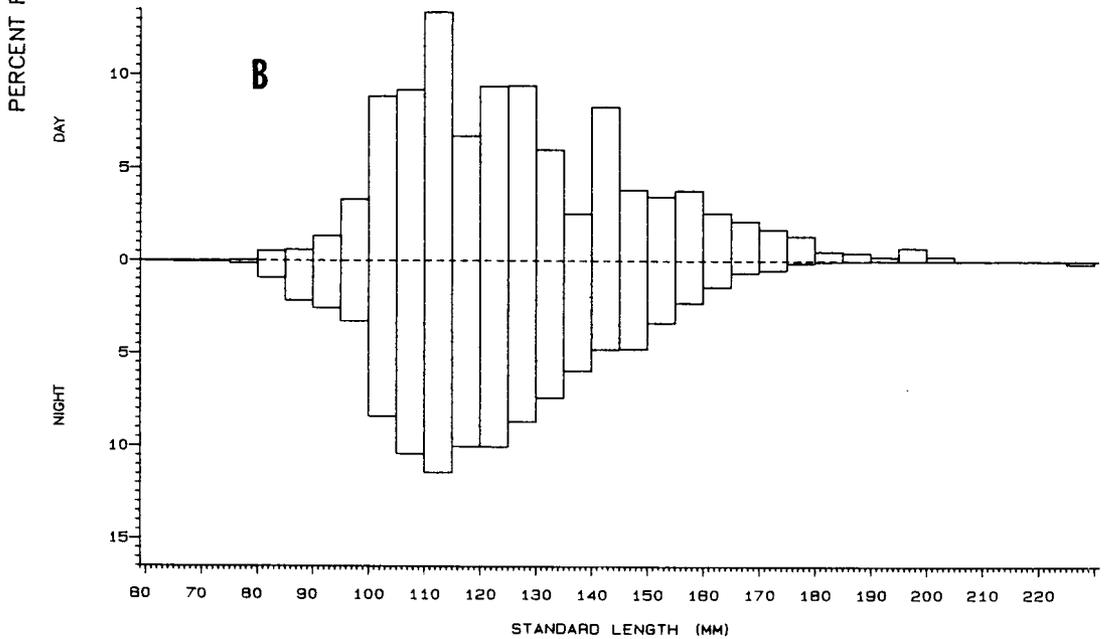
177

PERCENT FREQUENCY OF OCCURRENCE

IMMATURE QUEENFISH
SIZE FREQUENCIES
DAY 5-10M DEPTH N=9394   NIGHT 5-27M DEPTH N=3013
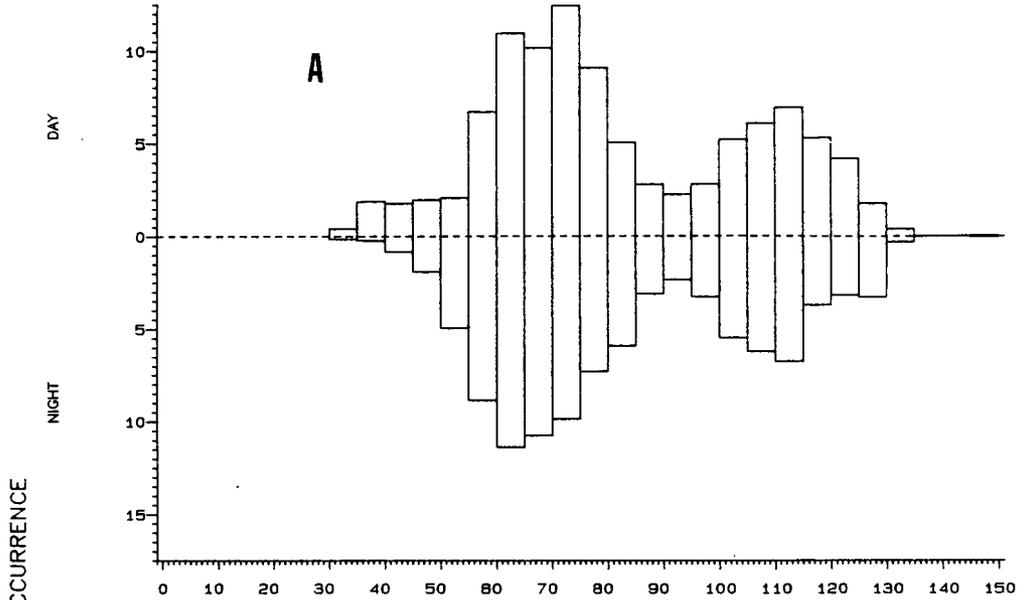
ADULT MALE QUEENFISH
SIZE FREQUENCIES
DAY 5-10M DEPTH N=3238   NIGHT 5-27M DEPTH N=3155

STANDARD LENGTH (MM)

178

ADULT FEMALE QUEENFISH
SIZE FREQUENCIES
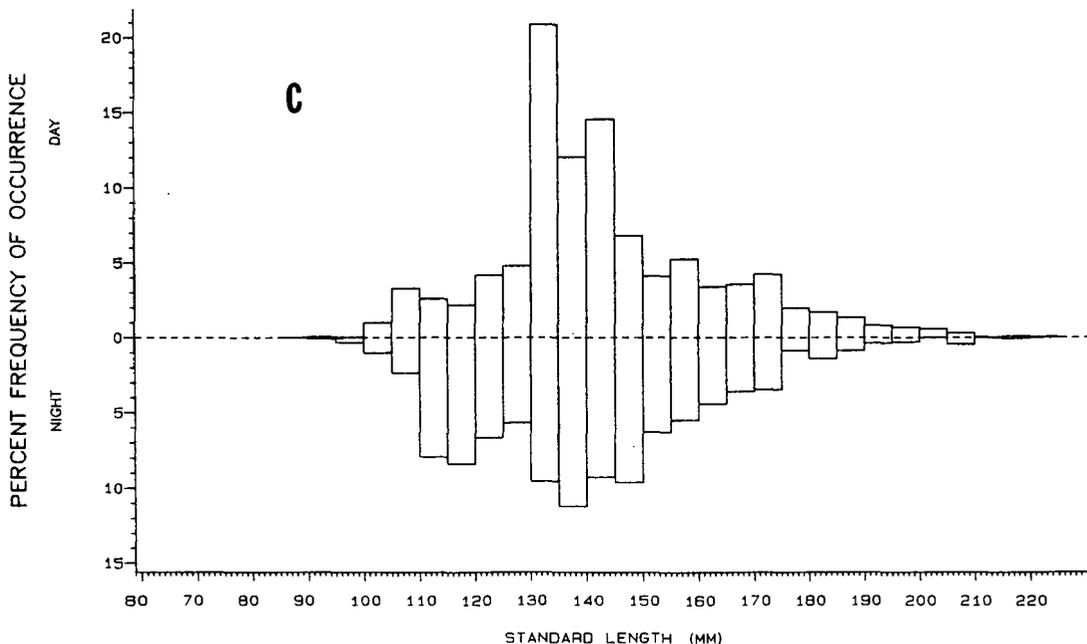DAY 5-10M DEPTH N=3292   NIGHT 5-27M DEPTH N=1286

FIGURE 4.—Relative length-frequency distributions of (A) immature, (B) adult male, and (C) adult female queenfish caught during the day in the shallow depth block versus during the night in all depth blocks pooled (see Figure 1 caption for details).

TABLE 3.—Results of Kolmogorov-Smirnov Two Sample comparisons of the diel- and depth-specific length-frequency distributions of queenfish caught during the onshore, breeding versus onshore, nonbreeding periods of year. Qualitative results of comparisons are noted.

	Breeding			Nonbreeding		
	D > N?	D_{max}	P	D > N?	D_{max}	P
Day vs. night, shallow depths						
Immatures	yes	0.37	<0.001	yes	0.10	<0.001
Adult males	yes	0.06	0.05	yes	0.10	0.05 > P > 0.01
Adult females	yes	0.28	<0.001	yes	0.25	<0.001
	Mid > Shal?	D_{max}	P	Mid > Shal?	D_{max}	P
Shallow vs. mid-depths, at night						
Immatures	yes	0.19	<0.001	yes	0.33	<0.001
Adult males	yes	0.32	<0.001	yes	0.12	0.05
Adult females	yes	0.15	0.01	no	0.14	>0.1

queenfish of both sexes, as well as immatures, fed to large extents on prey (Table 4) whose centers of abundance were shallow (see Discussion and Conclusions). For immatures such major prey included holoplankton (*Labidocera trispinosa*) and meroplanktonic cumaceans (primarily *Diastylopsis tenuis*) (Table 4). *Diastylopsis tenuis* and other nearshore crustaceans also comprised nontrivial fractions of the diet of adult queenfish during the periods of onshore depth distribution (Table 4). *Diastylopsis tenuis*, a night-active meroplankter characteristic of the shallow region (see below), also occurred in the stomachs of fish collected at shallow depths during the day and during the night at middepths. Hence we feel justified to characterize the queenfish diet using data for both diel periods and depth blocks pooled in Table 4. State of prey digestion, though, tended to be less at

TABLE 4.—Prey taxa comprising ≥1% of the diet (by IRI) of immature, adult male, and adult female queenfish during the two periods of onshore distribution combined. Sample fish collected during both day and night and at shallow (5-10 m) and middepths (11-16 m) are pooled (see text). Diet characterized by number (N), reconstructed wet weight (Wt), and frequency of occurrence (FO) of prey; overall contribution to diet evaluated by IRI (Pinkas et al. 1971). Prey ranked by IRI within queenfish categories. N = number of fish examined that had food in their stomachs. Mean (and range) of body lengths (SL, mm) of fish examined were immatures—70 (34-100), adult males—127 (76-210), and adult females—146 (102-214).

	Type of prey	% IRI	% N	% Wt	% FO	Mean Wt/ prey (mg)
Immatures (n = 57)						
Labidocera trispinosa	holoplanktonic copepod	35.8	26.7	3.2	56.1	<0.2
Acartia tonsa	holoplanktonic copepod	20.9	40.2	2.8	22.8	<0.1
Metamysidopsis elongata	meroplanktonic mysid	15.6	5.9	7.9	52.6	1.7
Engraulis mordax	clupeoid fish	9.0	1.1	11.6	33.3	13.7
Diastylopsis tenuis	meroplanktonic cumacean	5.1	3.6	3.2	35.1	1.1
Ogyrides sp.	? meroplanktonic caridean shrimp	2.4	<0.1	31.9	3.5	472
Atylis tridens	meroplanktonic amphipod	2.1	2.0	2.6	21.1	1.7
Acanthomysis macropsis	meroplanktonic mysid	1.3	0.6	2.2	21.1	4.7
Blepharipoda occidentalis	? meroplanktonic megalops/juvs. (anomuran)	1.0	0.2	9.0	5.3	53.0
All other prey		6.8	19.6	25.6	—	1.7
Adult males (n = 228)						
Engraulis mordax	clupeoid fish	74.6	6.3	89.0	47.8	385
Diastylopsis tenuis	meroplanktonic cumacean	7.1	18.4	0.9	22.4	1.3
Metamysidopsis elongata	meroplanktonic mysid	6.4	10.0	0.8	36.4	2.1
Labidocera trispinosa	holoplanktonic copepod	6.4	14.9	0.1	25.9	<0.2
All other prey		5.5	50.4	9.2	—	5.0
Adult females (n = 236)						
Engraulis mordax	clupeoid fish	78.9	5.7	90.8	52.1	783
Metamysidopsis elongata	meroplanktonic mysid	6.5	10.8	0.5	36.4	2.3
Diastylopsis tenuis	meroplanktonic cumacean	3.7	10.8	0.3	21.2	1.2
Labidocera trispinosa	holoplanktonic copepod	3.1	10.2	<0.1	19.4	<0.2
Acanthomysis sculpta	meroplanktonic mysid	1.4	6.1	0.5	13.6	3.6
Caridean shrimp	? meroplanktonic	1.0	3.4	0.6	15.7	8.7
All other prey		5.4	53.0	7.3	—	6.9

night for both immature and adult queenfish (Table 5), indicating that all sizes of fish fed primarily at night.

DISCUSSION AND CONCLUSIONS

Functions of Nocturnal Offshore Dispersal in Queenfish

Diel migrations of queenfish have been previously reported. Queenfish have been directly observed emigrating offshore at dusk from inactive daytime schools nearshore at Santa Catalina Island, one of the Channel Islands offshore of the southern California mainland (Hobson and Chess 1976; Hobson et al. 1981). Similar behavior has been noted by Hobson[5] in mainland waters off La Jolla, near San Diego. Allen and DeMartini (1983) have characterized the general pattern of nocturnal offshore dispersal of queenfish near San Diego. Direct observation (Hobson and Chess 1976; Hobson et al. 1981) and examination of stomachs of fish collected during the day and at night (Hobson and Chess 1976; Hobson et al. 1981; Allen and DeMartini 1983; this study) confirm the primarily nocturnal feeding habits of queenfish. A spawning function has also been implicated for the offshore movements of adult queenfish at dusk (DeMartini

TABLE 5.—Results of Spearman's rank correlations (Siegel 1956) between index of state of digestion of stomach contents and time of collection for immature, adult male, and adult female queenfish. All samples collected prior to midnight. Sample fish collected during day, night, and at shallow (5-10 m) and middepths (11-16 m) are pooled over both onshore periods of distribution (see text).

	Digestion versus time		
	rho	N	P
Immatures	−0.35	57	0.007
Adult males	−0.20	228	0.003
Adult females	−0.22	236	<0.001

and Fountain 1981). During the February-July/August spawning season, ripe females with ovaries in hydrated (ready-to-spawn) condition can be collected throughout the daylight period beginning 1 h after sunrise, while females collected as soon as 1 h after sunset are either ripening (but nonhydrated) or are recently spent (De-Martini and Fountain 1981).

The diel distributional (CPUE) data of this study (Fig. 1) clearly illustrate the differences in diel migration made by immature, adult male, and adult female queenfish. Size-composition data (Figs. 2-4) further characterize the diel migrations as related to size of fish, regardless of maturity state or whether adults in the populations were reproductively active.

Certain aspects of the diel CPUE data suggest a breeding function for offshore dispersal at night, since only the distribution of immatures remained centered onshore at night. Also, a disproportionately greater number of adult males versus females emigrated offshore at night (Fig. 1B, C). This is consistent with an offshore migration by females for spawning that occurs on a less frequent than daily basis, since individual female queenfish ripen and spawn batches of eggs on average only once a week (DeMartini and Fountain 1981). The male-biased, daytime aggregations of ready-to-spawn queenfish (DeMartini and Fountain 1981) suggest that individual males spawn at more frequent than weekly intervals. Also, preflexion stages of queenfish larvae are most abundant in midwaters over 12-45 m bottom depths from 1.9 to 5.4 km offshore in the region of San Onofre-Oceanside (Barnett et al.[6]), which strongly

suggests that most spawning occurs in outer nearshore regions.

Other distributional data, however, indicate a primarily feeding function for offshore dispersal at night. The nighttime, offshore shift in the distribution of adults of both sexes, for example, occurred during both the nonbreeding and breeding seasons. In addition, relatively more of the larger individuals among the immatures (as well as more of the larger adults of both sexes) moved offshore at night (Fig. 3) from the shallow region wherein queenfish of all sizes co-occurred during the day (Figs. 1, 4). The latter pattern persisted during both breeding and nonbreeding periods of year when distributions were generally inshore of 30 m bottom depth. On balance, the size composition of immature and adult female queenfish censused at 5-27 m depths at night resembled the composition of those censused at 5-10 m depths during the day (Fig. 4A, C), indicating that few very large immatures or females move offshore of 27 m at night. This moreover confirms that the queenfish seined offshore at night had resided at 5-10 m depths during the day and not in a region (e.g., shallower or deeper) that we did not census. Analogous data for adult males (Figs. 1, 4B) indicate that this may not be true for the largest males. However, the pattern of larger individuals farther offshore persisted for males as well as immatures and females during the nonbreeding period.

The diel food habit data also are largely consistent with the hypothesis that queenfish disperse offshore at night to feed, despite several discrepancies. Certain prey are known to be much more abundant at either extreme of the queenfish depth distribution. The presence of shallow-living "marker" species such as *Diastylopsis tenuis* (Table 6) in the stomachs of queenfish collected offshore of the respective prey distribution likely reflects some feeding activity just prior to or during the dusk offshore emigration. The presence of some night-active meroplankton in stomachs of fish collected during the day probably represents the partial confounding of nighttime foraging by circumdiel gut residence times. We consider it unlikely that queenfish feed on prey such as *D. tenuis* during the day, as the nocturnal activity patterns of this and other species of demersal meroplankton

TABLE 6.—Prey taxa comprising ≥1% of the diet (by IRI) of immature, adult male, and adult female queenfish collected during the night from the mid-depth (11-16 m) block. Data for the two periods of onshore distribution are pooled; for further details of diet characterization see Table 4. Mean (and range) of body lengths (SL, mm) were immatures—71 (42-86), adult males—126 (83-183), and adult females—147 (103-207).

	Type of prey	% IRI	% N	% Wt	% FO	Mean Wt/ prey (mg)
Immatures (n = 14)						
Engraulis mordax	clupeoid fish	25.2	2.6	27.2	42.9	16.8
Metamysidopsis elongata	meroplanktonic mysid	23.3	7.3	9.3	71.4	2.1
Acartia tonsa	holoplanktonic copepod	16.4	55.0	3.2	14.3	<0.1
Labidocera trispinosa	holoplanktonic copepod	15.0	16.2	1.6	42.9	<0.2
Ampelisca brevisimulata	? demersal amphipod	3.8	1.3	12.2	14.3	15.0
Diastylopsis tenuis	meroplanktonic cumacean	3.5	3.3	2.9	28.6	1.4
Acanthomysis macropsis	meroplanktonic mysid	3.1	1.3	4.2	28.6	5.2
Ampelisca cristata	? demersal amphipod	2.8	1.6	18.2	7.1	18.0
Blepharipoda occidentalis	? meroplanktonic juveniles (anomuran)	1.8	0.3	12.4	7.1	61.2
Hemilamprops californica	meroplanktonic amphipod	1.6	2.3	0.6	28.6	0.4
All other prey		3.5	8.8	8.2	—	1.6
Adult males (n = 125)						
Engraulis mordax	clupeoid fish	82.4	11.0	95.5	53.6	463
Labidocera trispinosa	holoplanktonic copepod	5.8	20.8	<0.1	19.2	<0.2
Metamysidopsis elongata	meroplanktonic mysid	4.0	8.4	0.4	31.2	2.3
Diastylopsis tenuis	meroplanktonic cumacean	3.2	12.2	0.3	17.6	1.3
All other prey		4.6	47.6	3.8	—	4.2
Adult females (n = 89)						
Engraulis mordax	clupeoid fish	83.6	9.1	93.0	59.6	615
Metamysidopsis elongata	meroplanktonic mysid	6.5	15.6	0.7	29.2	2.6
Diastylopsis tenuis	meroplanktonic cumacean	2.5	11.6	0.2	15.7	1.2
Labidocera trispinosa	holoplanktonic copepod	1.8	7.3	<0.1	18.0	<0.2
Hemilamprops californica	meroplanktonic amphipod	1.0	8.1	<0.1	9.0	0.4
All other prey		4.6	48.3	6.0	—	7.5

are well recognized (Barnard and Given 1961; Hobson and Chess 1976).

The significant amount of shallow-living prey such as *D. tenuis* and *Labidocera trispinosa* present in the stomachs of queenfish captured offshore at night (Table 6) nonetheless clearly illustrates that these fish had recently emigrated from depths nearer to shore. Numerous data characterize *D. tenuis* as largely restricted to within the 30 m isobath (Barnard and Given 1961; Parr and Diener[7]). *Diastylopsis tenuis*, in fact, declines >1 order of magnitude in abundance in benthic core samples between 8 and 15 m depths near San Onofre (Parr and Diener footnote 7). *Labidocera trispinosa*, a holoplanktonic copepod, also has been described as much more abundant inshore of 12-15 m bottom depths, both off La Jolla (Barnett 1974) and off San Onofre-Oceanside (Barnett et al.[8]). It seems less likely that nearshore forms such as *D. tenuis* and *L. trispinosa* are more available as prey offshore at night, since they are markedly less abundant offshore.

The presence of offshore prey in the stomachs of adult queenfish collected offshore obviously reflects nocturnal foraging while in that region.

Neomysis kadiakensis, a mysid more abundant at depths corresponding to those frequented by adult queenfish at night (Clutter 1967; Bernstein and Gleye[9]), was a nontrivial component of the diet of adult queenfish that ranked third by weight in both males and females (although <1% of the total IRI for each sex). None of the immature queenfish that we sampled, however, had eaten any *N. kadiakensis*, even its juvenile stages (which also occur offshore, Bernstein and Gleye footnote 9). Nearshore prey, such as *L. trispinosa* and the demersal meroplankter, *D. tenuis*, were generally more important by weight and frequency of occurrence, if not numbers, in the diet of immature versus adult queenfish (Table 4). The tendency for immatures to remain closer to shore than adults and to feed on meroplankton (that are more abundant in sheltered areas closer to shore) has been noted for many species of nocturnal zooplanktivorous fishes on tropical coral reefs (Hobson and Chess 1978).

Both immature and adult queenfish are concentrated nearshore during the day, probably in response to pressure from diurnal predators (Hobson 1978; Allen and DeMartini 1983). Several species of voracious carnivores including Pacific mackerel, *Scomber japonicus*; Pacific bonito, *Sarda chiliensis* (Allen and DeMartini 1983); and California halibut, *Paralichthys californicus*, of piscivore-size (Plummer et al. 1983) are less abundant nearshore in the San Onofre-Oceanside region. The California halibut is a known predator of queenfish (Frey 1971; Plummer et al. 1983). The kelp bass, *Paralabrax clathratus*, another species known to prey on queenfish (Young 1963; E. DeMartini[10]), is most abundant in and near beds of giant kelp, *Macrocystis pyrifera*, that occur at 10-15 m bottom depths in the region (Larson and DeMartini 1984).

Overall, our data indicate that the nocturnal offshore dispersal of adults and the less contagious distribution of immatures nearshore at night are primarily for feeding. Allen and DeMartini (1983) reviewed and discussed the possible advantages of dispersal for feeding in schooling, zooplanktivorous fishes. To these we add the possible benefit (for adult queenfish) of foraging in regions where *N. kadiakensis*, a species of large mysid, is more abundant. It is also likely that the rate at which individual queenfish encounter planktonic prey is enhanced by foraging in regions farther offshore, where longshore currents are, on average, stronger (Reitzel[11]).

The nighttime, nearshore distribution of small immature queenfish also may be due to either or both of the following factors. First, small queenfish are undoubtedly incapable of making as extensive diel migrations as adults because of body size limitations. Hence the nearshore daytime distribution of immatures, probably set primarily by the influence of diurnal predators offshore, might limit the offshore movements of immatures at night. Second, predation pressure from nocturnal predators located farther offshore could restrict immature queenfish to nearshore regions. Potential nocturnal predators of immature queenfish include California halibut (Allen 1982) and California scorpionfish, *Scorpaena guttata* (Hobson et al. 1981). The nocturnal habits of other potential predators (Pacific mackerel, Pacific bonito, and Pacific barracuda, *Sphyraena argentea*) of small, immature queenfish are unknown. Large (>70 mm SL, Fig. 3) immature queenfish move offshore to some extent at night, which is also consistent with offshore dispersal to feed on larger prey, since size of prey is strongly related to queenfish body size (Tables 4, 6). Offshore dispersal of large immatures is nonetheless consistent with relaxed predation pressure, since susceptibility to predation must be inversely proportional to body size.

Rigorous evaluation of offshore dispersal for spawning would require censuses of the onshore, offshore distribution of recent spawning products. However, we are at present unable to routinely distinguish queenfish eggs or yolk-sac larvae <2.2-2.3 mm long (~4 d old or less) (Watson[12]).

In summary, we conclude that, as might be expected, the distributional (including migration) patterns of queenfish have feeding, predator avoidance, and perhaps other functions such as breeding.

[9]Bernstein, B. B., and L. G. Gleye. The ecology of mysids in the San Onofre region. A study submitted to the Marine Review Committee of the California Coastal Commission, April 30, 1981. Unpubl. rep., 72 p. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

[10]E. DeMartini, Marine Science Institute, University of California, Santa Barbara, CA 93106. Unpubl. data.

[11]J. Reitzel. 1979. Physical/chemical oceanography. *In* Interim Report of the Marine Review Committee of the California Coastal Commission. Part II: Appendix of Technical Evidence in Support of the General Summary, March 12, 1979, p. 6-23. Unpubl. rep. Marine Review Committee Research Center, 531 Encinitas Boulevard, Suite 106, Encinitas, CA 92024.

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Comparison With
the Diel Migrations of Other Fishes

Numerous other temperate (see Hobson and Chess 1976; Hobson et al. 1981; Allen and DeMartini 1983) and tropical (reviewed in Helfman et al. 1982) fishes are known to make horizontal migrations at dusk and dawn away from and back to reefs and other shallow areas. Such migrations have been characterized as a form of commuting between daytime resting/sheltering and nighttime feeding areas (Hobson 1965, 1973). These behaviors are most widely recognized for tropical coral reef-based fishes that forage on night-active benthic invertebrates in surrounding sandflats and seagrass beds or on nocturnal meroplankton in the water column (Hobson 1965, 1973; Domm and Domm 1973; Helfman et al. 1982; and others). The diel migration of queenfish certainly suggests feeding as a major, if not principal function. Both predator avoidance and feeding are probably major determinants of the nearshore distribution of immature queenfish. Feeding is probably the principal reason for the crepuscular onshore, offshore migrations of adults. Offshore movement for spawning may be of secondary importance, but data are inconclusive.

With the exception of the relatively short-range (within-reef) migrations observed for some tropical wrasses (see Moyer and Yogo 1982 and others), we are unaware of any study of the diel migratory behavior of nearshore temperate or tropical fishes that has demonstrated a primary spawning function for the behavior. We do not now believe that spawning is a major reason for the nocturnal offshore movements of queenfish, although we still feel that spawning is partly involved. We strongly recommend that future studies of the diel migratory patterns of temperate and tropical fishes be watchful for possible spawning as well as feeding activity.

ACKNOWLEDGMENTS

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