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TRENDS IN ELEGANT TERN AND NORTHERN ANCHOVY POPULATIONS IN CALIFORNIA[1]

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Abstract. Elegant Terns (*Sterna elegans*) at San Diego had high reproductive success in 1980 and 1981; 86% of incubated eggs hatched, and over 97% of hatched chicks fledged. Tern chicks were most frequently fed northern anchovy (*Engraulis mordax*). Age compositions of anchovy samples taken from the commercial fishery and of those fed to chicks overlapped extensively, suggesting potential for competition for anchovies between nesting Elegant Terns and the fishery. Elegant Tern production was strongly correlated with anchovy abundance for 1979 to 1983.

Key words: Elegant Tern; Sterna elegans; *northern anchovy;* Engraulis mordax.

INTRODUCTION

Fishery managers have become increasingly aware that competition between man and birds for the same fish may have profound implications for all three groups (Idyll 1973, Furness 1982). The northern anchovy (*Engraulis mordax*) is the basic resource of a commercial fishery that is unregulated in Mexico and whose legal operating season in the United States (Huppert et al. 1980) overlaps the breeding season of seabirds in California. This anchovy is also an important food fish of game fishes, marine mammals, and several seabirds along the California coast and has been the predominant food of nestling California Brown Pelicans *Pelecanus occidentalis* (Anderson et al. 1980). Sunada et al. (1981) found that the age composition of anchovies taken by the fishery overlapped extensively with that of anchovies fed to Brown Pelican chicks. Furthermore, Anderson et al. (1982) found that Brown Pelican reproduction, measured by fledging success, was correlated with anchovy abundance.

Elegant Terns (*Sterna elegans*) formerly nested at about a dozen insular and coastal mainland sites in Baja California and the Gulf of California, Mexico (Bent 1921; Bancroft 1927a, 1927b; Banks 1963; Lindsay 1966). Several sites in central Baja California have been documented as recently as 22 years ago (egg sets at the Western Foundation of Vertebrate Zoology, Los Angeles, CA), but today only two breeding colonies are known. The larger colony is at Isla Raza in the central Gulf of California, Mexico, where about 10,000 pairs of Elegant Terns have bred per year in recent times (Walker 1965; E. Velarde, pers. comm.). The smaller colony, located 600 km north at San Diego Bay, California, is used by 400 to 900 pairs of Elegant Terns. Elegant Terns bred at San Diego for the first time in 1959 (Gallup and Bailey 1960). The establishment of that colony, a 500-km extension of the known breeding range of the species, followed the *El Niño*-Southern Oscillation event of 1957 to 1958 (Quinn et al. 1978). Colony establishment was coincident with an increase in anchovy abundance in waters off southern California and northern Baja California (Smith and Eppley 1982, Stauffer and Charter 1982).

The exceptional location and history of the Elegant Tern colony at San Diego, together with the overlap in use of northern anchovies by breeding Brown Pelicans and the fishery, indicated that a study of Elegant Terns might reveal a relationship between tern reproduction, northern anchovies, and the fishery. Herein, I examine this relationship by comparing the age composition of northern anchovies fed to Elegant Tern chicks to that of anchovies taken by the fishery and by comparing the patterns of tern reproduction with the variation in anchovy abundance.

STUDY AREA AND METHODS

The study site consisted of a series of dikes between salt-evaporating ponds at the south end of San Diego Bay, California (32°36′N, 117°07′W, Fig. 1; Ohlendorf et al. 1985, Schaffner 1985). The dikes sit 1 to 2.5 m above the spring water line and are 2 to 10 m wide; during summer, lower water levels expose silty beaches on the western (bay-side) edge of most dikes. Some dikes support patches of halophytic succulents and herbaceous plants. Dike substrates are soft silt, smooth hardpan, or clods of dried mud. Elegant Terns nested on all three substrate types during 1980 to 1983.

I visited the study site two to four times a week from late March to August of 1980 and 1981, but up to six times a week when hatching was likely to occur. I visited the study site approximately weekly from late March to Au-

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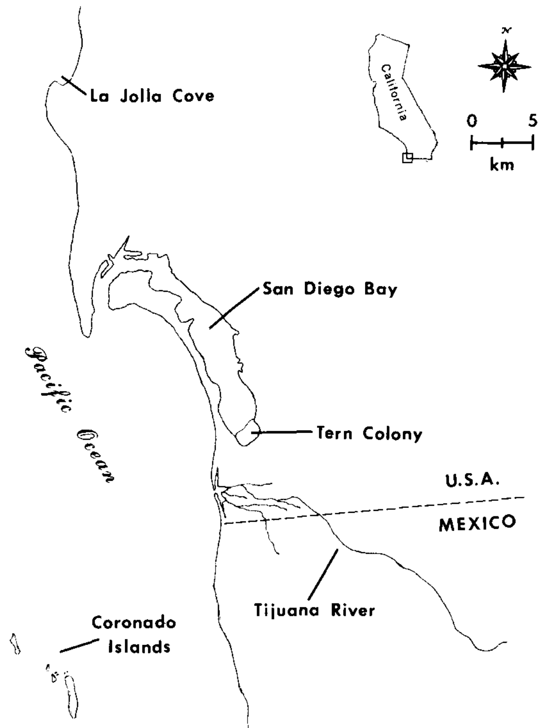

FIGURE 1. Location of the tern colony in south San Diego Bay, California, in relation to surrounding areas.

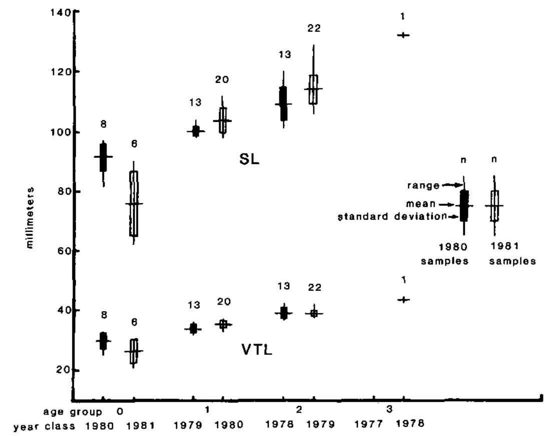

FIGURE 2. Length distributions by age group and year class of whole northern anchovies taken from Elegant Tern food samples in 1980 and 1981. VTL = vent-to-tail length; SL = standard length.

gust of 1982, but with as many as three visits during some weeks. During 1983, I made ten visits between mid-April and late June. The duration of these visits varied between five and nine hours.

Elegant Terns nested in several subcolonies (subcolony = all nesting groups on a given dike), and I was able to examine all nests in the colony on each visit in 1980. In 1981 and 1982, subcolonies were more widely placed, so I typically examined a portion of the colony on one visit, the remainder on the next visit, and the entire colony on a third visit. I examined the entire colony on seven of the ten visits in 1983.

In 1980 and 1981 I assessed reproductive performance from all known nests in the colony, except for 51 that were used for experimental manipulations (Schaffner 1982). I determined colony size by direct examination of all known nesting areas, and I made direct counts of nest scrapes, eggs, and chicks. Fewer visits in 1982 and 1983 prevented me from determining colony status, except the number of nests attended throughout the incubation period.

In 1980 and 1981 I determined food species by collecting chick regurgitations and fishes dropped at nest and crèche sites. I collected chick regurgitations by approaching crèches on foot and increasing my walking speed until the chicks began to run. When I approached within a few meters, the chicks stopped, emptied their crops, and fled. I collected regurgitations and herded the crèche back to its original location. No crèche was moved more than 30 m in one direction and none was sampled more than once per week. I seldom handled adults and thus did not sample food fishes from them.

Because one of the crèches of 1981 was located on a nest site area during its first two weeks, some of the fish sampled from the crèche site might have been dropped there before any hatching had occurred. In general, crèche-site collections may represent fishes accidentally dropped by adults and chicks or fish rejected by chicks (see Hulsman 1981, Atwood and Kelly 1984) and therefore probably reflect the diet of Elegant Terns less accurately than do chick regurgitations.

I placed food samples in plastic bags and immediately transported them to San Diego State University (SDSU) for preliminary identification. I fixed all species except northern anchovies in 10% formalin, then stored all specimens in 70% ethanol and identified them. Northern anchovies were not fixed, to avoid opaquing of otoliths (see below). I identified fishes using Miller and Lea (1972) and the SDSU reference collection. I measured whole northern anchovies from crèche sites and chick regurgitations to the nearest mm standard length (SL, from snout to base of tail), and vent-to-tail length (VTL, from anterior edge of vent to base of tail). I also measured VTL for incomplete (=head end digested) northern anchovies.

I removed otoliths from whole northern anchovies, examined them in water at 20 × under a binocular dissecting microscope, and determined fish age by counting annuli (Fitch 1951,

TABLE 1. Reproductive performance of Elegant Tern nests monitored in 1980 and 1981. Data exclude 51 experimental nests in each year.

	1980	1981
Mean clutch size[a]	1.02 (648/636)	1.02 (939/924)
No. of one-egg clutches	624	909
No. of two-egg clutches	12	15
Min. no. of breeding pairs[b]	571	823
No. of eggs	580	837
No. of chicks hatched	570	814
Proportion hatched[c]	88.0% (570/648)	86.7% (814/939)
No. of nests hatching young	563	801
No. of chicks fledged	554	794
Proportion fledged/hatched	97.2%	97.5%
Proportion fledged/eggs laid in nests	85.5%	84.5%

[a] Represents the total number of eggs laid in nests divided by the number of nest attempts; excludes unsuccessful first nesting attempts by 112 pairs in 1980 (complete data not available).
[b] Represents nests attended throughout the incubation period (min. 25 days).
[c] Equals the number hatched divided by the number of eggs laid in nests, excluding unsuccessful first nesting attempts by 112 pairs in 1980.

Collins and Spratt 1969). SL and VTL distributions by otolith-determined age group and year class are given in Figure 2. These data formed the basis for the VTL-age scale I used for headless anchovies. Resulting data for anchovies from crèche-site collections and chick regurgitations were combined for comparison to aged northern anchovies sampled from the commercial catch landed at Terminal Island, California. I used fishery data for June of each year, when the majority of the Elegant Tern samples was collected. Legal restrictions on mesh size of nets prevent the fishery from taking anchovies of Age Group 0 (Huppert et al. 1980, MacCall et al. 1983).

The uniformly high hatching and fledging success of Elegant Terns in 1980 and 1981 and the nearly uniform one-egg clutch size (see Results below) permitted me to use the number of breeding pairs as an indirect estimate of Elegant Tern production. The measure of anchovy abundance chosen for comparison with tern production was the estimate of spawning biomass, projected from larval censuses, for the northern anchovy central subpopulation (or central stock) between 30°N and 38°N (Huppert et al. 1980, Smith and Eppley 1982, MacCall et al. 1983). Elegant Terns are present throughout this latitudinal range at various times of the year (Bent 1921, Cogswell 1977, Garrett and Dunn 1981).

RESULTS

REPRODUCTIVE PERFORMANCE AND COLONY SIZE

In 1980 through 1983 egg laying occurred from the first week of April through the first week of June, parental care of chicks from the first week of May through the end of July, and fledging from the first week of June through the end of July. Elegant Terns nested in three subcolonies in 1980 and four subcolonies in 1981. In 1980 the earliest subcolony, with 112 pairs, was established 7 to 9 April, located in a roosting area of several hundred Western Gulls (*Larus occidentalis*) and Ring-billed Gulls (*L. delawarensis*). The gulls destroyed all tern eggs within five days. Six days later another subcolony of 109 pairs of terns formed on an adjacent dike. Most of these pairs were probably from the subcolony whose initial nesting attempt had been destroyed. In 1980 and 1981 the number of nests added to previously (and synchronously) established nesting groups was similar to the number of nests (clutches) destroyed during the previous 6 to 10 days of that year. These observations suggest that most pairs that failed in their initial nesting attempt renested.

Hatching and fledging success were high in 1980 and 1981, with 86% of incubated eggs hatching and at least 97% of hatched chicks surviving to fledging (Table 1). There were two crèches in 1980 and four in 1981, one per surviving subcolony.

The minimum number of breeding pairs equaled the total number of clutches initially incubated minus the number destroyed. In 1980 through 1982, the number of nests (clutches) attempted each year was about 13% higher than the estimate of minimum number of breeding pairs in that year (Table 2). With the assumption of renesting by all initially unsuccessful pairs, this estimate of minimum number of breeding pairs yields the most useful index of population size because it is similar to estimates from counts of nest scrapes just before hatching (as in 1983) or just after hatching (as in 1979).

FOOD SAMPLES

The fishes I collected from the nest site areas in 1980 (Table 3) were small and unlikely to be important components of the Elegant Tern

TABLE 2. Counts related to breeding population size at the San Diego Elegant Tern colony 1979 through 1983. Data are for the entire colony.

	1979	1980[a]	1981	1982	1983
Total eggs laid	—	762	1,098	—	—
No. of eggs abandoned[b]	—	69	108	50+	35+
Total nest attempts[c]	—	687	975	904	—
No. of eggs	—	699	990	926	—
Min. no. of breeding pairs[d]	450[e]	607	861	801	437
No. of eggs	—	616	875	823	443

[a] Data exclude the unsuccessful first nesting attempt by 112 pairs that subsequently renested en masse.
[b] Includes eggs abandoned, laid in Caspian Tern nests, or laid at crèche sites (none of which were incubated).
[c] Nests that were attended at least 24 hr.
[d] Nests that were attended throughout the incubation period (min. 25 days).
[e] M. U. Evans, pers. comm.

diet. Most of these tiny fishes were likely used in highly ritualized pair-bond maintenance "feeding" of adult females by males and were similar to those used at courtship-club sites away from the colony shortly before waves of synchronous nesting. The ritual feeding at Elegant Tern club sites, in fact, seldom utilized real fish. Often some bit of debris was substituted, or the characteristic courting, precopulatory and copulatory behaviors were performed with nothing in the bill (Schaffner 1982).

There were significant differences in the proportions of the nest site, crèche site, and chick regurgitation collections composed by northern anchovies ($G = 11.95$; $P < 0.05$; df = 1). Nest site collections in 1981 (Table 3) contained many more northern anchovies than in 1980 ($G = 79.00$; $P < 0.05$; df = 1), including some incomplete and whole anchovies from four regurgitated boluses I collected before any hatching had occurred. This suggests that adults were feeding on northern anchovies. Northern anchovies were the single most abundant species collected at crèche sites (Table 4), though they were relatively more common in 1980 than in 1981 ($G = 6.23$; $P < 0.05$; df = 1). One of the four 1981 crèches was located

TABLE 3. Collections of fishes from nest sites.

Species	Year[a]	Mean standard length of whole fish ± SD (cm)	Total no. of specimens collected[b]	% of the year's total nest-site collections
Engraulidae				
Anchoa spp.	1980	5.7 ± 0.41	16 (16 + 2)	15.4
	1981	6.4 ± 1.47	35 (26 + 9)	19.9
Engraulis mordax	1980	4.1 ± 1.50	10 (7 + 3)	9.6
	1981	10.9 ± 0.44	107 (14 + 93)	60.1
Atherinidae				
Atherinops affinis	1980	4.1 ± 0.54	58 (49 + 9[c])	55.8
	1981	5.2 ± 1.70	12 (6 + 8)	6.8
Leuresthes tenuis	1980	—	—	—
	1981	10.5 ± 0	1 (1 + 0)	0.6
Gobiidae				
Gillichthys mirabilis	1980	4.0 ± 1.11	13 (13 + 0)	12.5
	1981	6.7 ± 1.25	7 (7 + 0)	3.9
Embiotocidae	1980	5.2 ± 0.67	7 (7 + 0)	6.7
	1981	6.1 ± 1.32	5 (5 + 0)	2.8
Syngnathidae				
Syngnathus leptorhynchus	1980	—	—	—
	1981	16.4 ± 1.10	6 (1 + 5)	3.4
Bothidae				
Paralichthys californicus	1980	—	—	—
	1981	4.5	1 (1 + 0)	0.6
Crustaceae	1980	—	—	—
	1981	[d]	2	1.1

[a] Year of collection.
[b] Number of whole fish plus number of headless fish indicated in parentheses.
[c] *Atherinops affinis* 1980 headless fish measured 2.0 to 6.7 cm.
[d] Length of thorax and tail together equals 4.5, 6.7 cm.

TABLE 4. Collections of food fishes from crèche sites. "Whole" *Engraulis mordax* are those whose otoliths were readable.

Species	Year[a]	Mean standard length of whole fish ± SD (cm)	Total no. of specimens collected[b]	% of the year's total crèche-site collections
Engraulidae				
Anchoa spp.	1980	6.5 ± 0.20	3 (2 + 1)	4.9
	1981	6.5 ± 1.70	30 (18 + 12)	20.1
Engraulis mordax	1980	10.1 ± 0.85	34 (19 + 15)	55.1
	1981	10.0 ± 1.27	55 (29 + 26)	36.9
Atherinidae				
Atherinops affinis	1980	9.1 ± 1.18	14 (13 + 1)	23.0
	1981	7.6 ± 2.95	31 (22 + 9)	20.8
Leuresthes tenuis	1980	11.2 ± 1.14	2 (2 + 0)	3.3
	1981	14.7 ± 0	3 (1 + 2)	2.0
Gobiidae				
Gillichthys mirabilis	1980	5.8 ± 1.26	3 (3 + 0)	4.9
	1981	6.0 ± 2.02	14 (14 + 0)	9.4
Embiotocidae	1980	6.4 ± 0.97	5 (5 + 0)	8.2
	1981	7.6 ± 1.53	7 (6 + 1)	4.7
Syngnathidae				
Syngnathus leptorhynchus	1980	—	—	—
	1981	5.9 ± 0	1 (1 + 0)	0.7
Bothidae				
Paralichthys californicus	1980	—	—	—
	1981	5.9 ± 0	1 (1 + 0)	0.7
Sternoptychidae				
Argyropelecus sladeni	1980	—	—	—
	1981	5.8 ± 0	1 (1 + 0)	0.7

[a] Year of collection.
[b] Number of whole fish plus number of headless fish indicated in parentheses.

on a nest-site area during its first two weeks. Northern anchovies were significantly more abundant in the chick regurgitations of 1981 than 1980 (Table 5; $G = 27.24$; $P < 0.05$; df = 1). Northern anchovies were the most frequently encountered fish in five of the six collection categories and they constituted a majority of fish in four collection categories.

FORAGING

During the 1980 through 1983 breeding seasons, longjaw mudsuckers (*Gillichthys mirab-*

TABLE 5. Collections of food fishes from chick regurgitations. "Whole" *Engraulis mordax* are those whose otoliths were readable.

Species	Year[a]	Mean standard length of whole fish ± SD (cm)	Total no. of specimens collected[b]	% of the year's total regurgitations collected
Engraulidae				
Anchoa spp.	1980	8.0 ± 0	1 (1 + 0)	9.0
	1981	—	—	—
Engraulis mordax	1980	10.2 ± 0.78	60 (45 + 15)	58.3
	1981	11.3 ± 0.91	138 (118 + 20)	86.8
Atherinidae				
Atherinops affinis	1980	6.9 ± 2.78	19 (10 + 9)	18.4
	1981	9.1 ± 4.00	10 (3 + 7)	6.3
Leuresthes tenuis	1980	10.8 ± 0.55	10 (3 + 7)	9.7
	1981	12.6 ± 0.60	9 (2 + 7)	5.7
Gobiidae				
Gillichthys mirabilis	1980	5.6 ± 0.98	6 (6 + 0)	5.8
	1981	3.6 ± 0	1 (1 + 0)	0.6
Embiotocidae	1980	5.4 ± 0.56	7 (7 + 0)	6.8
	1981	5.7 ± 0	1 (1 + 0)	0.6

[a] Year of collection.
[b] Number of whole fish plus number of headless fish indicated in parentheses.

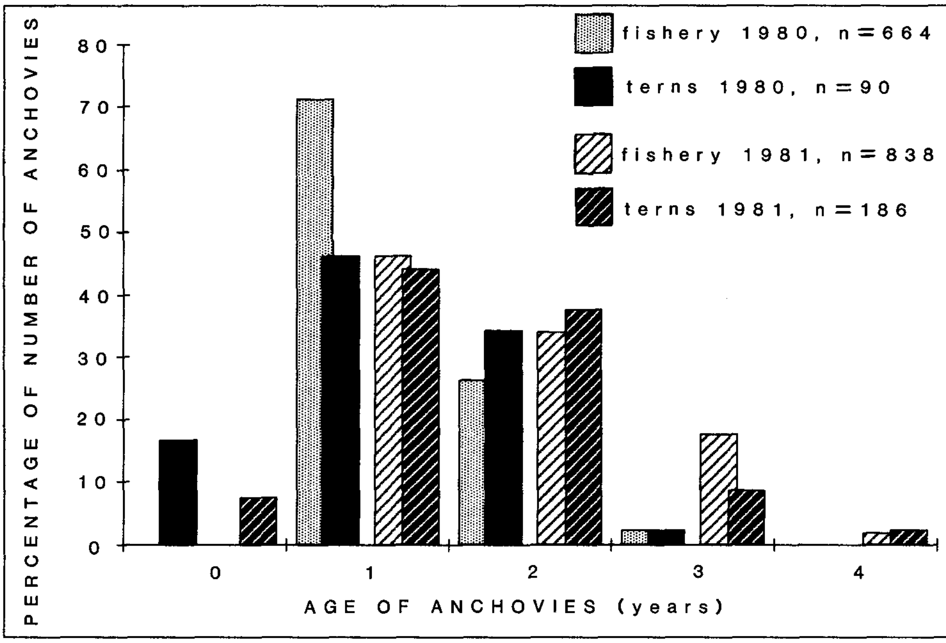

FIGURE 3. Age composition by numbers of fish of northern anchovies taken from Elegant Tern and commercial fishery samples in June 1980 and June 1981.

ilis) and topsmelt (*Atherinops affinis*) were common in some of the salt ponds surrounding the dikes on which the terns nested. These species, as well as slough and deepbody anchovies (*Anchoa delicatissima* and *A. compressa*), were local common estuarine and inshore fishes (Miller and Lea 1972). *Gillichthys mirabilis, A. affinis,* and *Anchoa* spp. were sometimes captured by Elegant Terns at two siphons that bring water into the saltworks from the bay, and the former two species were occasionally captured by Elegant Terns diving from small flocks that hovered over foraging Double-crested Cormorants (*Phalacrocorax auritus*) and striped mullet (*Mugil cephalus*) in two of the salt ponds.

During the peak period of chick care (mid-June), flight paths of Elegant Terns were very predictable. At dawn Elegant Terns streamed out of the colony singly or in groups of two to seven, headed west across the south end of the bay to the coast, and then turned south and followed the beach to the mouth of the Tijuana River. From the river mouth they turned southwest heading offshore toward the Coronado Islands. Returning birds usually carried a single large northern anchovy crosswise in the bill. The return route to the colony was from the Coronado area to the mouth of the Tijuana River then north, often direct and over land. Thus an anchovy fed to a chick might represent 50 km of travel for the provisioning parent. Elegant Terns sometimes foraged in several bays immediately before and after the breeding seasons of 1980 through 1983, particularly at the mouth of San Diego Bay and La Jolla Cove (Fig. 1). However, they did not use these areas during the breeding seasons, nor were they commonly seen foraging within 8 km of the breeding colony.

AGES OF NORTHERN ANCHOVIES

The overall age compositions of the tern and fishery anchovies (of Age Groups 0 to 3+) for both 1980 and 1981 showed significant within-year differences ($G = 284$; $P < 0.05$; df = 9; Fig. 3). Both the tern and fishery samples showed between-year differences also (tern: $G = 11.6$; fishery: $G = 152$; both *P*s < 0.05; df = 3 for each).

For anchovies of Age Groups 0 to 3+, there were significant differences between the tern and fishery samples for each year (1980 and 1981, $G = 72.6$ and 55.9; *P*s < 0.05; df = 2 for each).

For anchovies of age groups which could be taken by both the terns and the fishery (Age Groups 1 to 3+ only), there were no differences between the two samples for each year (1980 and 1981, $G = 5.67$ and 0.44; *P*s > 0.05; df = 2).

In addition, for anchovies of Age Groups 1–3+, in both the tern and fishery samples, abundance decreased with increasing age group within each year (Spearman rank correlation $r_s = 1.00$; $P < 0.01$; $n = 3, 3, 3, 3$; Siegel 1956), and changes in age composition between years were in similar directions (Fig. 3).

ELEGANT TERN BREEDING POPULATION SIZE AND ANCHOVY ABUNDANCE

Elegant Tern numbers and anchovy abundance were significantly correlated (Spearman rank correlation, $r_s = 1.00$; $P < 0.01$; $n = 5$; Siegel 1956) for 1979 through 1983, the years for which adequate data exist. The initial nesting of Elegant Terns at San Diego (1959) was coincident with an apparent increase in anchovy abundance (Fig. 4) and anomalously warm oceanic conditions (Lasker and MacCall 1983, MacCall 1984).

DISCUSSION

Length distributions of northern anchovies taken by Elegant Terns are smaller at each age than previously reported in the literature (e.g., Collins and Spratt 1969, Huppert et al. 1980). However, anchovies have been consistently smaller in each age group since about 1978 (Lasker and MacCall 1983:118). The smaller anchovy size reflected in the data for the San Diego site is also consistent with its location on the fringe of the United States and northern Mexican fishery areas, where anchovies are smaller at each age than more northerly anchovies (MacCall et al. 1983: figure 4.2-1).

The minor differences in age composition between tern and fishery anchovies may reflect differences in foraging areas. The fishery data are for the catch landed roughly 150 km north of the tern colony. These may accurately characterize the fishery area in general, but a higher proportion of Age Group 1 anchovies has been sampled from the northern Mexican catch (R. Methot and T. Barnes 1982, unpubl.). This suggests that the actual age composition of tern and fishery anchovies may be more similar than my data suggest (Fig. 3). Elegant Terns are strictly surface feeders, whereas the fishery can capture anchovies to a depth of at least 30 m. Thus, the fishery is less sensitive to differences in patterns of vertical distribution between age groups of anchovies.

The reduced peak in the Elegant Tern population of 1981 when compared to anchovy abundance (Fig. 4) may suggest that nearly all of the colony's potential breeders nested that year.

A striking feature of the relationship between the Elegant Tern and the northern anchovy is its similarity to the relationship between the California Brown Pelican and the northern anchovy (Anderson et al. 1980, 1982; Sunada et al. 1981). These similarities include the following: (1) both Elegant Terns and Brown Pelicans in southern California are highly dependent on northern anchovies when feeding chicks, (2) the age composition of anchovies taken by the fishery greatly overlaps with those

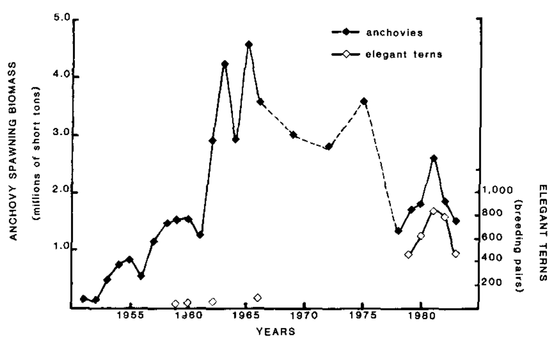

FIGURE 4. Estimated spawning biomass for the central subpopulation of northern anchovies and numbers of breeding pairs of Elegant Terns at San Diego for the years 1951 through 1983. Sources: anchovies—Stauffer and Charter 1982 (1951 through 1981), Picquelle and Hewitt 1983 (1982), Picquelle and Hewitt 1984 (1983); terns—Emblen 1954 (1953); Gallup and Bailey 1960 (1959); Small 1960 (1960), G. Collier, pers. comm. 1980 (1962), Kirven 1969 (1966), M. U. Evans, pers. comm. 1980 (1979), this study (1980–1983). Broken line indicates where fishery observations were not annual. Values for 1979 through 1983 are: anchovies, 1.723, 1.775, 2.803, 2.060, and 1.510 million short tons. Values for terns are: 450, 607, 861, 801, and 437 breeding pairs.

of anchovies fed to chicks, and (3) reproduction of the birds varies with anchovy abundance. The data presented here for 1981 particularly emphasize the importance of anchovies to Elegant Tern reproduction, as anchovies constituted over 86% of the chick regurgitations when population size peaked.

The extensive overlap in age compositions of the Elegant Tern and fishery samples suggests that they are using similar resources and that potential for competition exists (see Furness 1982). An alternative view is that anchovies constitute an enormous resource pool for which both the terns and the fishery are nonselective samplers, taking each age group in proportion to its abundance, with little opportunity for competition. By analogy, the latter view seems less likely. Fisheries have typically had detrimental impacts on fish and seabird populations (Idyll 1973, Ainley and Lewis 1974, Furness 1982, MacCall 1984). In California, the Pacific sardine was overfished to near extinction four decades ago (Murphy 1968), and northern anchovy spawning biomass and recruitment continue to decline (MacCall et al. 1983, Hewitt 1984). In light of the lesson of the Pacific sardine, these declines are cause for concern and close watch of the southern California and northern Mexico seabird and northern anchovy populations by ornithologists.

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