

# THE INVASION OF *SAURIDA UNDOSQUAMIS* (RICHARDSON) INTO THE LEVANT BASIN – AN EXAMPLE OF BIOLOGICAL EFFECT OF INTEROCEANIC CANALS

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## ABSTRACT

The Red Sea lizardfish, *Saurida undosquamis* (Richardson), invaded the Levant Basin and established a population of considerable commercial importance. Its expansion came at the expense of other commercial fishes on which it preys and with which it competes. The explosion of the Red Sea lizardfish population in the Levant Basin was made possible by a combination of changes in the environmental conditions (abiotic and biotic), one of these being the retreat of, or the recession in, the native hake population. The dynamic coexistence between the lizardfish and the hake, its main competitor, is affected by fluctuations in the abiotic conditions to which the hake seems to be more sensitive than the lizardfish.

A faunistic, zoogeographical approach to the marine animal migration through the Suez Canal is common to most investigators of the canal's influence. Animal species native to one sea and found in the other after the opening of the canal serve as main indicators of its biological influence and of its effectivity as a link to the migrant species and as a barrier to others (Ben-Tuvia, 1966, in press; Kimor, 1970<sup>3</sup>; Por, 1971; Steinitz, H., 1968; Steinitz, W., 1929; Thorson, 1971). Many authors listed and described migrant species (Barash and Danin, 1971<sup>4</sup>; Ben-Tuvia, 1953; Collette, 1970; Gilat, 1964; Gohar, 1954; Gordin, 1966<sup>5</sup>; Holthuis and Gottlieb, 1958; Kosswig, 1951; Steinitz, H., 1967; Tortonesi, 1953).

Some authors have discussed the Red Sea-Mediterranean animal migrations in relation to ecological conditions in the canal and in the adjacent sea areas (Gilat, 1966<sup>6</sup>, 1969<sup>7</sup>; Oren, 1969,

1970; Por, 1969<sup>8</sup>, 1971<sup>9</sup>), suggesting that the mechanism of the penetration of some species through the canal and their expansion in the Mediterranean is associated with environmental conditions (salinity, currents, nature of substrate, etc.).

In this paper we discuss the ecology of the migration and expansion in the new habitat of an important commercial fish. We examine its dynamic coexistence with its native competitor in view of the changing environmental conditions.

## The Relative Importance of Species

It is a well-known fact that, while some of the migrant species have established themselves in the new environment, creating populations with a significant impact on the ecosystem, other species may just survive under the new and, perhaps, hostile conditions.

The relative importance of a species in terms of biomass and its role and weight in the food chain is often neglected when two species are listed as "common" or "abundant." One of them may be an important commercial fish with a biomass of an order of tens of thousands of tons or more, and the

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<sup>3</sup>Kimor, B. 1970. The Suez Canal as a link and a barrier in the migration of planktonic organisms. Submitted to the Ocean World-Joint Oceanographic Assembly, Tokyo, 13-25 Sept. 1970, 20 p.

<sup>4</sup>Barash, A., and Z. Danin. 1971. Indo-Pacific species of Mollusca in the Mediterranean. Appendix to Progress Report 1970/1971. The Hebrew University - Smithsonian Institution Joint Project "Biota of the Red Sea and the Eastern Mediterranean," 8 p. [Processed.]

<sup>5</sup>Gordin, H. 1966. Migration of fishes through the Suez Canal. Ms. in files of Fish. Technol. Unit, Haifa, Israel.

<sup>6</sup>Gilat, E. 1966. The animal bottom communities in the Levant Basin of the Mediterranean Sea. 9 p. In files of Fish. Tech Unit, Haifa. [Processed.]

<sup>7</sup>Gilat, E. 1969. The macrobenthic communities of the level bottom in the Eastern Mediterranean. In Interim Report, Joint Research Project "Biota of the Red Sea and the Eastern Mediterranean," p. 82-89. The Hebrew University of Jerusalem and the Smithsonian Institution, Washington, D.C. [Processed.]

<sup>8</sup>Por, F. D. 1969. The Canuellidae (Copepoda Harpacticoida) in the waters around the Sinai Peninsula and the problem of Lessepsian migration in this family. In Interim Report, Joint Research Project "Biota of the Red Sea and the Eastern Mediterranean," p. 34-40. The Hebrew University of Jerusalem and the Smithsonian Institution, Washington, D.C. [Processed.]

<sup>9</sup>Por, F. D. 1970. The nature of the Lessepsian migration through the Suez Canal. Paper presented at the XXIIe Congrès Assemblée Plénière de la C.I.E.S.M., Rome.

other is, say, a frequently met small, commercially unimportant, *Apogon*. However, such discrimination should be made: the first fish is a wholesale consumer and also a supplier of important food for other species; the other, although frequently collected, occurs in small numbers, and whatever its importance may be in its immediate biotope, its effect on the whole ecosystem is of little consequence. Therefore, in studying the impact of one sea on the other, number of migrant species should not be overemphasized and more attention should be paid to species of ecological importance.

### Commercial Fish Populations as Indicators of the Biological Effect

The most important aspect of interrelations between two seas, especially where a new canal is planned, are the ecological effects which influence the human ecological conditions and economy. To obtain a meaningful picture of the biological effect of the Suez Canal on both seas, emphasis should be put on changes which have considerably affected the large or the commercial populations of either. Obviously, almost any fish species which occurs in great numbers and biomass becomes sooner or later commercially important, either as a marketable product or as a food to commercial piscivores.

Changes in the quantity and composition of important commercial fishes are contained in most fisheries statistics. Of course, this can only be shown where fish landings are reasonably well recorded and where the data obtained may be evaluated to eliminate technological and socioeconomical factors.

### Commercially Important Red Sea Migrants and Their Mediterranean Competitors

A number of immigrant Red Sea species have become commercially important in the Levant Basin and/or provide food for both Red Sea immigrants and native fish populations. Sufficient data are available to discuss the expansion of the Red Sea lizardfish, *Saurida undosquamis* (Richardson), and the dynamics of its coexistence with its main native competitor *Merluccius merluccius* (Linnaeus), the hake.

Unfortunately, other species which could serve perhaps as better examples, the yellow-striped goatfish, *Upeneus moluccensis* Bleeker, and its Mediterranean counterpart the red mullet, *Mullus barbatus* Linnaeus, or the barracudas,

*Sphyræna chrysotaenia* Klunzinger (a Red Sea migrant), *S. sphyræna* (Linnaeus), and *S. viridensis* Cuvier (both Atlantic species), cannot be used for this purpose as the catch statistics do not discriminate between the species of the same family or genus.

From the information available on the Mullidae (*Upeneus* and *Mullus*), the following can be summarized: Red mullets (Mullidae) represent one of the most important components of the Israeli trawl catches. Their share in the total trawl landings varied between 1956 and 1970 from 29 to 46%, (Sarid, 1951-71). The bulk of the red mullets consists of two species: the red mullet and the yellow-striped goatfish. The latter species is a Red Sea migrant. According to Wirszubski (1953) in the late 40's the share of the yellow-striped goatfish in the Mullidae catch was 10 to 15%. Four years later, Oren (1957) estimated on the basis of Gilat's unpublished data that *Upeneus* formed over 83% of the total number of red mullets caught in trawls during the first half of 1956.

These are two closely related fish species, very similar in their appearance and behavior and apparently competing for the same food (E. Gilat, pers. comm.). Although the red mullet evidently prefers cooler and, thus, in periods, deeper waters than the yellow-striped goatfish (Ben-Yami, 1955; Ben-Tuvia, in press), they mostly occupy overlapping territories. One of them—the invader—succeeded in becoming a majority during 1955 (Ben-Yami, 1955; Oren, 1957). Since 1956, fluctuations continue to occur in the *Mullus* to *Upeneus* ratio. Ben-Tuvia (in press) estimates the average share of the latter fish in the catches of red mullets to be approximately 30%.

What are the reasons for such fluctuations? What are the factors which determine whether a fish which has crossed the canal will establish itself as a sizeable population?

Is it possible that after some years of blooming a migrant population will recede into its previous state, and why? Will an expanding migrant population contribute to the total fish biomass in the new area, or come at the expense of the other fishes?

### SOURCES AND RELIABILITY OF DATA

#### Fishery Statistics

All fisheries data presented in the graphs and

tables are based on statistics collected by the Department of Fisheries (Sarid, 1951-71). These are in general reliable, and the proportion of the hake and the lizardfish in the total trawl catch is well represented. The figures, however, may be biased in some aspects, and the following must be borne in mind:

1. The catch per unit effort for all fish and for each of the two species separately is expressed in kilograms per day at sea of a trawler. The Israeli trawlers operating in the Mediterranean during 1950-70 were powered by 110-to 240-horsepower engines. The average power per trawler varied with time, due to transfer of some to the Red Sea, loss of others, and acquisition of new vessels and engines. It increased steadily in the 50's, decreased in the early 60's, and started increasing again during the recent years (Table 1). Therefore, when examining the data in Figure 5A and B, it should be remembered that the unit of effort varied from year to year.

2. The total fishing effort and the total catches fluctuated partly because of the changing socioeconomical and geopolitical conditions, which determined the extent of the fishing grounds on which the Israeli trawlers could operate in the Mediterranean, and its effect on the size of the active trawling fleet.

3. The character and extent of the trawling grounds available to and/or preferred by the

fishermen partly affect the data: In deepwater operations the hake is one of the main fish caught (Ben-Yami, 1971; Zismann, 1971), while the lizardfish is almost absent. In shallow water, trawling depends on the accessibility of the southern trawling grounds, which fluctuated with the Egypto-Israeli relations. On these grounds good summer catches could be obtained in shallow waters, conditions preferred by some skippers to deepwater trawling.

From 1953 to 1960, some of the Israeli trawlers operated during the summer months in the north-eastern area of the Mediterranean, between Cyprus and Turkey, mostly in the Bay of Tarsus. Their catches were included indiscriminately in the general statistical data. In these catches, the lizardfish greatly outweighed the hake. Therefore, the catch composition data for these years may be slightly biased in favor of the lizardfish and to the disadvantage of the hake as compared with the other years, but by no means to a degree which might change the general picture.

## Sea Temperature

In order to study effects of changes in the environmental factors on the catches of the hake and the lizardfish, the temperatures recorded from the sea between Ashdod and Tel Aviv, an area

TABLE 1.—Changes in the fishing effort, catch and catch-per-effort, 1950-1970, in the Israel Mediterranean trawling fishery.<sup>1</sup>

Year	Number of trawlers	Horsepower		Number of days at sea	Catch total of the selected boats (tons)	Catch/100 hp per day (kg)
		Total	Average per trawler			
1950	7	840	120	976	312	265
1951	19	2,420	127	3,102	1,031	211
1952	14	2,070	146	2,152	667	221
1953	14	2,070	146	2,728	997	250
1954	17	2,350	139	3,047	1,160	273
1955	22	3,120	142	3,523	1,494	298
1956	16	2,530	158	2,616	1,162	281
1957	16	2,520	158	3,185	1,335	225
1958	20	3,020	151	4,350	1,575	239
1959	23	3,330	145	5,208	1,878	235
1960	17	2,580	152	3,386	1,077	208
1961	15	2,130	142	2,957	874	295
1962	14	1,990	142	2,694	766	284
1963	13	1,760	135	2,505	647	191
1964	10	1,390	139	1,765	530	215
1965	13	1,800	138	2,443	676	200
1966	13	1,840	141	2,579	561	155
1967	14	2,010	143	2,933	720	195
1968	14	2,070	147	2,985	925	210
1969	14	2,140	153	2,967	979	224
1970	14	2,290	163	3,013	886	180

<sup>1</sup>The data do not include research and training vessels, and vessels which fished less than 100 days per year (E. Groft, private communication).

situated in the center of the trawl grounds, were examined.

The water temperatures at, or closely below, the 75-m depth (Figure 1), and a number of sea surface temperatures were collected during monthly cruises of Israeli research vessels (Oren and Hornung, 1972, and pers. comm.). During the 21 yr,

many monthly cruises were not carried out, hence the numerous gaps (Figure 2).

Additional surface temperature data for the period from 1958 to 1970 are monthly averages of daily monitored temperatures at Ashdod. These were supplied by the Coast Study Division of the Israel Port Authority (pers. comm.).

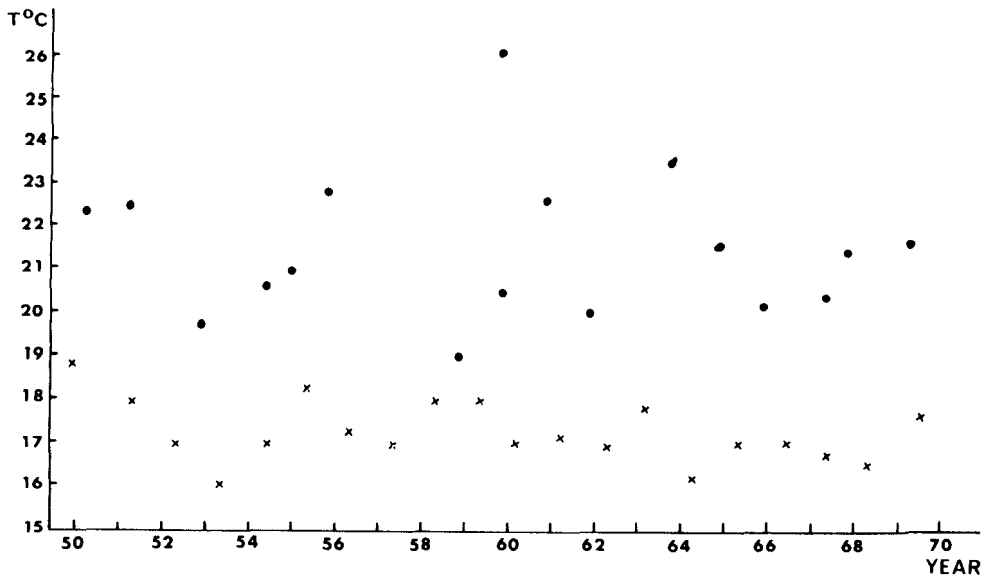


FIGURE 1.—Sea temperatures at depths of 75 m or below, collected during monthly cruises in or near the Tel Aviv-Ashdod area between 1950 and 1970 (Oren and Hornung, pers. comm.). Dots - yearly maxima; cross - yearly minima. In this graph each year begins in January.

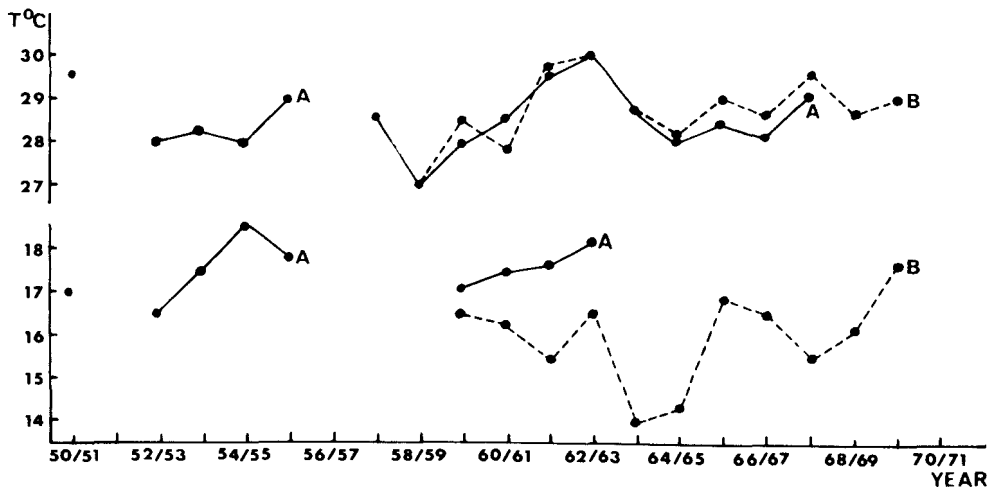


FIGURE 2.—Sea surface temperature. Top - summer maxima; bottom - winter minima. A - Data collected during monthly cruises in the area of Tel Aviv-Ashdod (Oren and Hornung, pers. comm.); B - (dashed line)—monthly means of daily collected data at Ashdod, inshore (Coastal Survey Unit, pers. comm.). Each year starts 1 September.

### Meteorology

Air temperature (monthly averages) and precipitation data for 1950-70 were published by the Israel Meteorological Service. These data are complete and uninterrupted for the whole period. Only those data which were collected at stations between Tel Aviv and Ashdod (Anonymous, 1950-71) were chosen (Figures 3, 4).

### Presentation

In attempting to find the relationship between climatic phenomena and fish catches, it is simpler to follow a calendar based on seasons with the year

beginning in the fall, at the beginning of the rainy season in this area. Thus, for the purpose of this study, the environmental and most of the fisheries data are given according to years which start on 1 September and end on 31 August, i.e., 1 September 1950-31 August 1951 forms the year 1950/51.

In some instances, extreme values rather than annual averages may be influential factors affecting crops or populations. One year may be a rainy year, but most of the rains may not have been timely, etc. For this purpose, some data are presented selectively to emphasize the more critical points. Thus, e.g., the average of the three coldest months, whatever these months may be in each

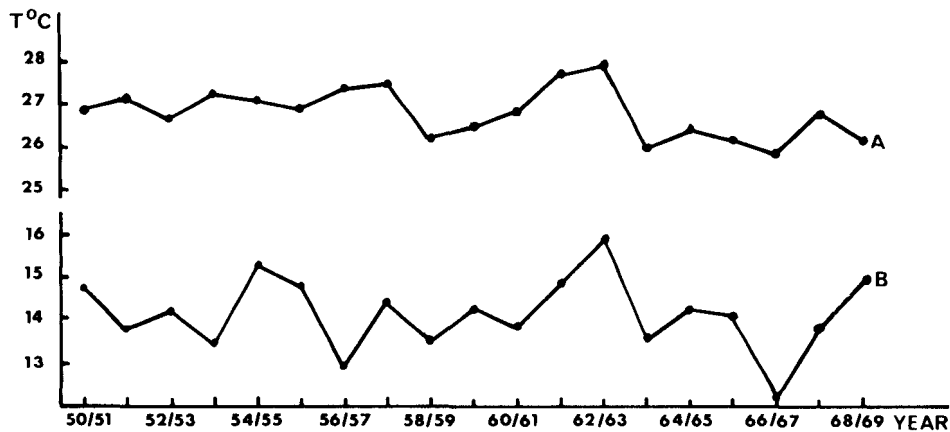


FIGURE 3.—Air temperatures, 1950/51-1968/69 (Anonymous, 1950-70). A - Summer maxima, mean of the warmest month; B - average of three coldest months. Each year starts 1 September.

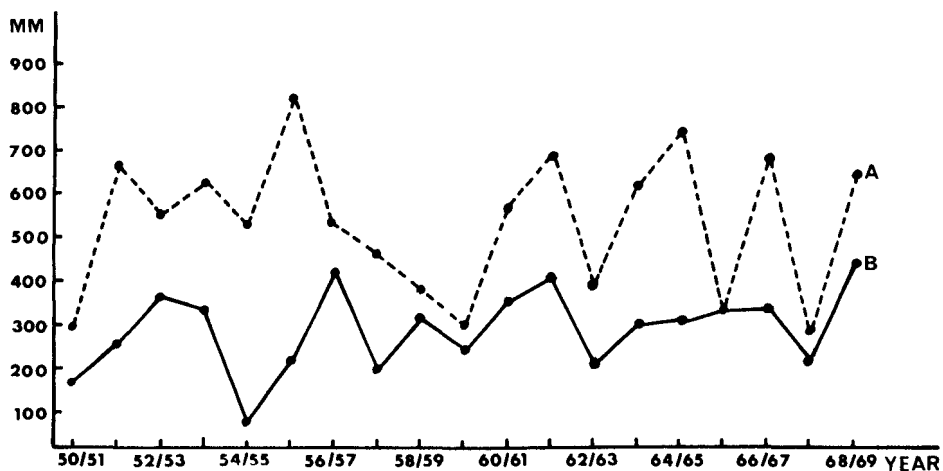


FIGURE 4.—Precipitation, 1950/51-1968/69 (Anonymous, 1950-70). A - September-January; B - January-April. Each year starts 1 September.

year, rather than the annual averages are used. Neither the data presented in this paper nor other available pertinent data have been statistically processed. Therefore we have limited ourselves to seek only most general patterns based on the most obvious dramatic changes and to point out apparent or likely correlations.

## THE RED SEA LIZARDFISH

### The Invasion

Prior to 1954, two species of lizardfish (Synodontidae) occurred rather infrequently in the catches of the Israeli Mediterranean trawlers: *Synodus saurus* (Linnaeus), a tropical Atlantic and Mediterranean species (Fowler, 1936), and the Red Sea lizardfish, an Indo-Pacific species. The latter was first reported from the Mediterranean as *Saurida grandisquamis* (Gunther) by Ben-Tuvia (1953, in press), who found it for the first time in December 1952. At that time, neither species was of commercial value, and *S. undosquamis* was much rarer than *Synodus saurus* (Ben-Tuvia, 1953, in press; Oren, 1957).

Ben-Tuvia (in press) observed that as early as August 1953 the lizardfish was fairly common in trawl catches taken in the Gaza-El Arish area, with 10 to 20 specimens caught usually in each haul.

In the winter of 1954-55, together with other changes in the composition of trawl catches, the proportion of the Red Sea lizardfish increased to such an extent that the fishermen attempted to market them as a food fish (Ben-Yami, 1955). Consequently, in 1955 lizardfish appeared for the first time in the statistics of landings (Sarid, 1956).

In the summer of 1955, unusual numbers of fingerlings were found in the cod ends of trawl nets. The bulk of them consisted of two Red Sea species, the yellow-striped goatfish and the lizardfish (Ben-Yami, 1955).

In 1955-56, the lizardfish became one of the main commercial fishes in Israel; its proportion in the total landings of Israel's marine fishery reached 11% (Sarid, 1956), and in the trawl fishery landings approximated 20% (Figure 5). Catch data collected during 1955 and 1956 (Oren, 1957) indicate that the Red Sea lizardfish made its first significant appearance in the trawl catches in the fishing grounds off the Gaza Strip and North Sinai. By the end of summer and autumn of 1955

it had expanded all over Israel's fishing grounds.

During the period 1952-60, most Israeli trawlers fished in the summer months in the north-eastern part of the Mediterranean (Gulf of Tarsus and neighboring waters). The Red Sea lizardfish, however, was not found in those waters in 1952 by Gottlieb and Ben-Tuvia (1953), who produced a detailed list of 52 fish species caught in a trawl catch. By summer 1956, it was common in the trawl catches in the Bay of Tarsus (Ben-Tuvia, pers. comm.), and since then it has become well established and is one of the most important commercial fish in that area.

The quantity of lizardfish caught by the trawlers continued to increase until 1959 when almost 400 tons (20% of the total trawl catch) were landed (Sarid, 1960). This was followed by a 4-yr recession. In 1963, the catches dropped to an approximately 120-ton low, and since then, they apparently stabilized near this level with "normal" annual fluctuations.

### Food and Habitat of the Red Sea Lizardfish

The lizardfish is a demersal piscivore. Its food in the Levant Basin was studied by Bograd-Zismann (1965) and by Chervinsky (1959). Bograd-Zismann examined some 1,500 stomachs, of which 859 contained food. Of these, 77.3% contained fish; the rest contained invertebrates, mostly crustaceans, and digested matter. Chervinsky examined some 500 stomachs, of which 131 contained identifiable food. Large invertebrates were found in only 16 stomachs; the rest contained fish. Both authors indicate that the most frequent prey of the Red Sea lizardfish are clupeoid fish—according to Chervinsky (1959) anchovy, and according to Bograd-Zismann (pers. comm.) mostly anchovy, but also some sardines.

The second important group in the food of the lizardfish are fish of the family Mullidae (Bograd-Zismann, 1965; Chervinsky, 1959). Other important groups in the lizardfish food are Gobiidae, Centranchidae (listed as Maenidae by Bograd-Zismann, 1965, and by Chervinsky, 1959), and *Leiognathus klunzingeri* (Steindachner) (Bograd-Zismann, 1965; Chervinsky, 1959; Ben-Tuvia, 1966).

No direct information is available on the diurnal-nocturnal feeding activity of the lizardfish in the Levant Basin. Nonetheless, the high proportion of anchovy in the food of the

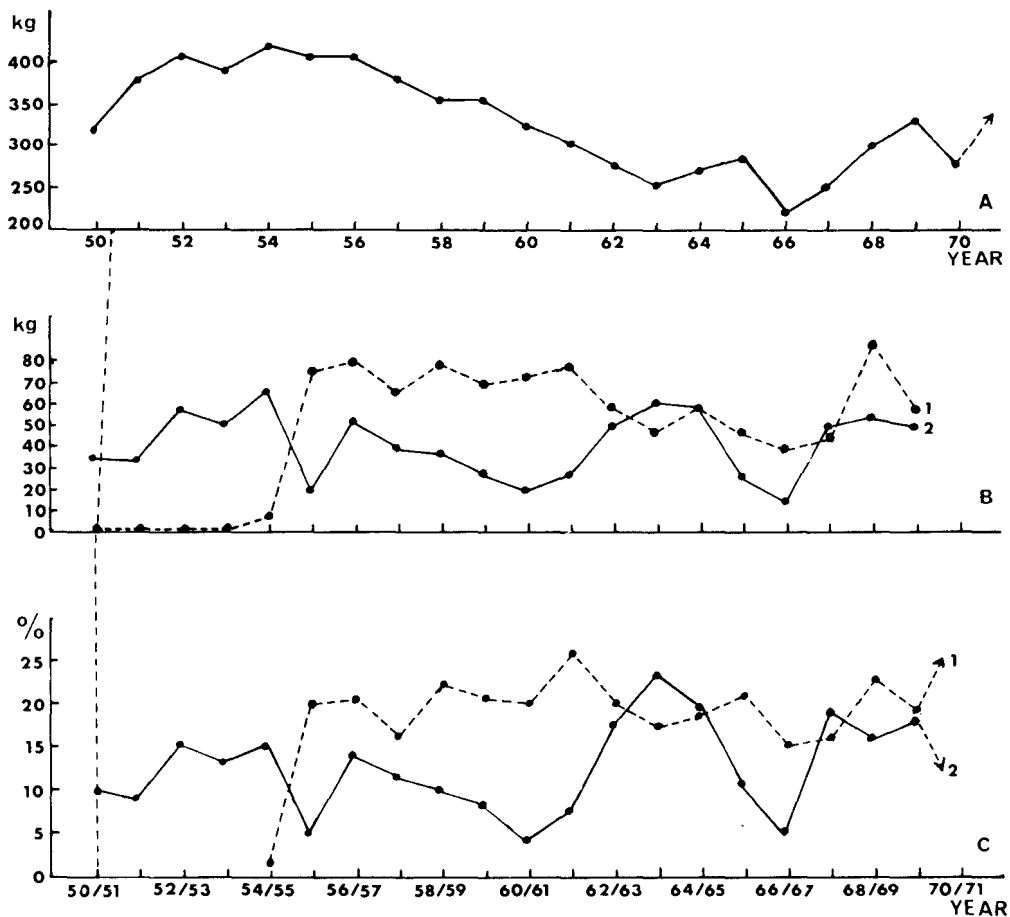


FIGURE 5.—Changes in the hake—Red Sea lizardfish relationship in catches and the catch-per-unit-effort (cpu) in the Israel trawl fishery in the Mediterranean, 1950-70 (Sarid, 1951-71). A - cpu—all fish, each year starts 1 January; B - cpu—(1) lizardfish, (2) hake; C - proportion in catch, percent: (1) lizardfish, (2) hake. B and C—each year starts 1 September.

lizardfish may indicate that either the lizardfish is a demersal feeder, feeding on clupeoids only when it approaches the bottom of the sea during the hours of light, or that it ascends during the night to the upper water layers where it could feed on these pelagic fish. We favor the first hypothesis, for the lizardfish almost never occurs in the night catches of purse seines in light fishing. This hypothesis is corroborated by observations of Hiatt and Strasburg (1960) of two lizardfishes, *Saurida gracilis* and *Synodus variegatus*, of the Marshall Islands. The lizardfish lie motionless, on or partly buried in the sand, and are virtually impossible to detect. Only when small fish come within a distance of a few feet, the lizardfish seize them in a rapid dart. They were rarely ob-

served to ascend for more than 3 to 4 feet while attacking their prey.

Hayashi, Yamaguchi, and Hanaoka (1960) and Tōriyama (1958) reported on the basis of stomach examinations that *S. undosquamis* in Japanese waters feeds during most hours of day and night. According to Tōriyama, however, feeding activity is most intensive during the early morning hours.

According to Chervinsky (1959), the lizardfish is cannibalistic. Bograd-Zismann (1961-62) observed that the occurrence of lizardfish in stomachs may rather be a result of panicky indiscriminate attacking in the trawl cod end.

The Red Sea lizardfish in the Levant Basin prefers rather shallow waters. It is caught in the cooler seasons at depths generally not exceeding 45 fm

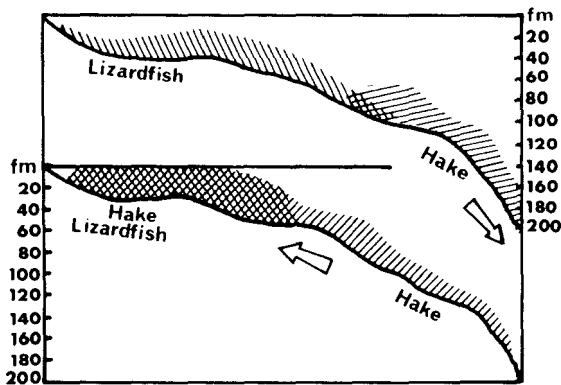


FIGURE 6.—The overlapping habitats of the Red Sea lizardfish and the hake over the Israel continental shelf. Top - summer; bottom - winter. Depth in fathoms.

(fathoms), but mostly at less than 35 fm (Figure 6). During the warm season the lizardfish may spread over deeper trawling grounds. Occasionally it occurs in catches made at 80 to 100 fm. In general, however, the lizardfish is of no commercial significance over the deepwater trawling grounds (Ben-Yami, 1971; Zismann, 1971).

### Spawning

There is very little biological information on the Red Sea lizardfish in this area. Bograd-Zismann (see footnote 10) and Chervinsky (1959) found that ripe, nearly ripe, and partly spent females occur in catches almost all year long, though the former author indicated that the greater proportion of nearly ripe females occurs in the early summer. It has to be borne in mind that a fish may spawn over a prolonged season, while the survival of its fry may be confined to a much shorter period controlled by favorable, seasonal conditions.

The area of spawning can only be speculated as being offshore and in deep water. This is based on the following information: Neither larvae nor juveniles of *Saurida* were taken during an extensive survey of fish larvae made using neuston nets (Ben-Yami et al., 1970) and Isaacs-Kidd mid-water trawl off the coast of Israel and Sinai during 1967-69. This survey consisted of 25 cruises covering inshore (Haifa Bay, Bardawil Lagoon), shal-

low water, and offshore stations. Only once, in December 1968, were *S. undosquamis* fry taken: nine 11-20 mm specimens were caught in deep water in the Isaacs-Kidd trawl, at a station situated 7 miles west of Cape Carmel, over 200 fm depth (Lourie, Herzberg, and Ben-Yami, 1969<sup>11</sup>; Lourie, pers. comm.).

The very fact that *S. undosquamis* larvae and juveniles did not occur either among the thousands of fish larvae and juveniles caught in neuston nets during day and night tows (Lourie et al., see footnote 11; Lourie, pers. comm.) or in samples taken by means of a light trap for small photokinetic organisms (Zismann, 1969) seems to indicate that they do not occur in the surface water layer, neither during the day nor by night. On the other hand, the capture of the young in December, over deep water and apparently deep in the mid-water, coincided with the seasonal temperature increase at this level (Oren, 1970) (Figure 1).

### Growth

Chervinsky (1959) has measured the length frequency of the lizardfish between June and December 1957, concluding that while the bulk of the lizardfish catch consisted of fish between 16 and 24 cm long, they grew fast; 2 cm per month. No males exceeding 24 cm were found, although females exceed 30 cm.

Bograd-Zismann (see footnote 10) examined the scales of the lizardfish. Two annuli were found on the scales of fish 22 to 30 cm total length (TL). On the scales of fish 19 to 22 cm TL, one annulus was seen, but there are indications that the year's growth is not marked by a clear annulus. Thus, it seems that the age of the lizardfish at recruitment is about 2 yr or may be 3 yr, the bulk of the fish in the catch being at least 2 yr old.

### Relation with Relative Species

To complete the ecological picture of the Red Sea lizardfish, its relationship with two of its relatives should be mentioned: one is the Atlantic-Mediterranean lizardfish, *Synodus saurus*, and

<sup>10</sup>Bograd-Zismann, L. 1961-62. Interim report on the study of the food of *Saurida undosquamis* in the Mediterranean Sea. Unpubl. manuscript. In files of the Isr. Sea Fish. Res. Stn., Haifa.

<sup>11</sup>Lourie, A., A. Herzberg, and M. Ben-Yami. 1969. A survey of neustonic fishes off the Mediterranean coast of Israel and Sinai, 1968. In Interim Report, Joint Research Project "Biota of the Red Sea and the Eastern Mediterranean," p. 133-150. The Hebrew University of Jerusalem and the Smithsonian Institution, Washington, D.C. [Processed.]



the other is the Indo-Pacific species greater lizardfish, *Saurida tumbil* (Bloch). The first is a quantitatively insignificant and hence noncommercial demersal predator in the Levant Basin. Although a natural competitor to the latter, the native *S. saurus* was superseded by the invader, being now as rare as ever.

*Saurida tumbil* is one of the main commercial fishes and dominates in the south Red Sea trawl fishery. Another species, *S. undosquamis*, is the "underdog" there, though not as rare as *Synodus saurus* is in the Levant Basin. *Saurida undosquamis* holds ground only in deeper and, evidently, cooler waters, while *S. tumbil* dominates over most of the trawling grounds (Ben-Tuvia, 1966). On the other hand, it is *S. undosquamis*, probably the euryecous of the two, which spread into the northern Red Sea, becoming the only significant lizardfish in the Gulf of Suez and the Levant Basin.

## HAKE

Another important commercial fish whose habitat and food in the Levant Basin indicate that it is the main competitor of the lizardfish is the hake, *Merluccius merluccius*. This is an eastern Atlantic species which is also native to these waters (Ben-Tuvia, 1953), and whose biology and habits in the Levant Basin still remain to be studied.

In the Atlantic Ocean the hake is known as a voracious predator, feeding during the day at the bottom and rising at night into higher water layers. It is known as a deepwater species caught at depths down to 400 fm. Off the British Isles, it seems to prefer water temperatures of around 10°C.

## Spawning and Growth

Near the British Isles, the hake spawns mostly at or near areas over the 100-fm isobath. Females spawn up to a million eggs each. The eggs are pelagic, floating on the sea surface. Before hatching, which occurs within a fortnight, the eggs descend to midwater, where the larvae hatch and develop. The yolk is absorbed within 3 to 4 wk after which the postlarvae feed on zooplankton. The fry descend to the bottom, where hake 3 to 4 cm long were taken. They reach 10 cm at the year's end and become mature at 20 cm (Marshall, 1965; Travis Jenkins, 1954).

## Feeding in Israel Waters

Shmida (1964)<sup>12</sup> investigated 76 stomachs of which 49 contained food. The fish were from catches taken in summer and spring. While the bulk of the food taken in spring consisted of crustaceans (mostly Decapoda, Macrura), the food of hake caught in summer was mostly fish. Shmida concludes that, in general, the food in terms of weight was half crustaceans and half fish. All identifiable fish were anchovy. Unfortunately, Shmida had at his disposal only small individuals, less than 27 cm long. Larger, faster, and stronger hake may have a different diet in which the proportion of fish may be higher. This was indicated by a slight trend of more fish in the stomachs of the larger hake, even within the narrow length range investigated (Shmida, 1964).

## Habitat

The hake prefers cool water. This is evident from its occurring over the shallow trawling grounds only during the cooler season of the year. Its proportion in trawl catches can be considerable, even at depths less than 20 fm, if the water is cold enough. With the approach of the warm season, the hake retreats to the deepwater regions where it remains available to trawls at depths over 100 fm throughout the season (Ben-Yami, 1971). Figure 6 illustrates the relative distribution of the lizardfish and the hake over the Israeli continental shelf and their overlapping habitats.

## RED SEA MIGRANTS AS PREY OF THE HAKE AND THE LIZARDFISH

As mentioned above, both our predators feed extensively on anchovy. It seems, nevertheless, that the hake competes with the lizardfish also for other fish, some of them Red Sea migrants. Ben-Tuvia (1966) reports that two of them, *Leio-gnathus klunzingeri* and a Red Sea goatfish, *Upeneus asymmetricus* Lachner (reported previously as *U. tragula* Richardson), are components of the food of both the lizardfish and the hake. *Leio-gnathus*, a trash fish in trawl catches, has been, undoubtedly, of major importance in the food

<sup>12</sup>Shmida, A. 1964. T'zumat dagim b'Yam Tikohn uv'Yam Suf (Food of fishes in the Mediterranean and the Red Sea). [In Hebrew.] Unpubl. manuscr. In files of the Isr. Sea Fish. Res. Stn., Haifa.

chain of demersal piscivores (Ben-Tuvia, 1966), and has declined (Ben-Tuvia, in press b) since its peak bloom in the 50's. Ben-Tuvia attributes this decline to the spread of the lizardfish, one of its main predators. The *U. asymmetricus*, usually small, does not occur in commercial quantities, and in the catches it is classified with the other red mullets.

Another Red Sea migrant, the yellow-striped goatfish, *Upeneus moluccensis* has not yet been identified from the stomachs of the hake. There are good indications that, ecologically, both the *Upeneus* and the lizardfish are closely related in a prey-predator relationship. They occupy the same habitat, the goatfish being an equally rare visitor at the deepwater trawling grounds (Zismann, in preparation). Both species seem to increase in catches during the same years (Ben-Yami, 1955; Oren, 1957), which may be associated with environmental conditions.

It is, thus, very likely that in areas where they are both found, the hake and the Red Sea lizardfish compete for food.

## THE MECHANISM OF AN INVASION

### Ecological "Barriers" to Migrating Species

A demersal fish expanding from one sea to another through a man-made canal encounters several barriers which it must overcome before a significant population can be established in the other sea (Figure 7). The "height" of an ecological barrier differs for each separate species. Hypersalinity, e.g., which may be prohibitive to some purely marine species, may not be a barrier or may even possess attractive environmental qualities to euryhaline organisms. The height of an ecological barrier may also change with seasonal, annual, and multiannual fluctuations in the environmental conditions.

The first barrier is the canal itself which may represent a less or more hostile environment for the migrating species. Migration through the Suez Canal must have been very difficult for some and impossible for other species, because of the complex hydrological conditions in the canal (the high salinity of the Bitter Lakes, freshening of the water due to influx of fresh water at some places, and the seasonal Nile floods) (Oren, 1970; H. Steinitz, pers. comm.). The nature of the Suez Canal, as a barrier, has changed, however, with

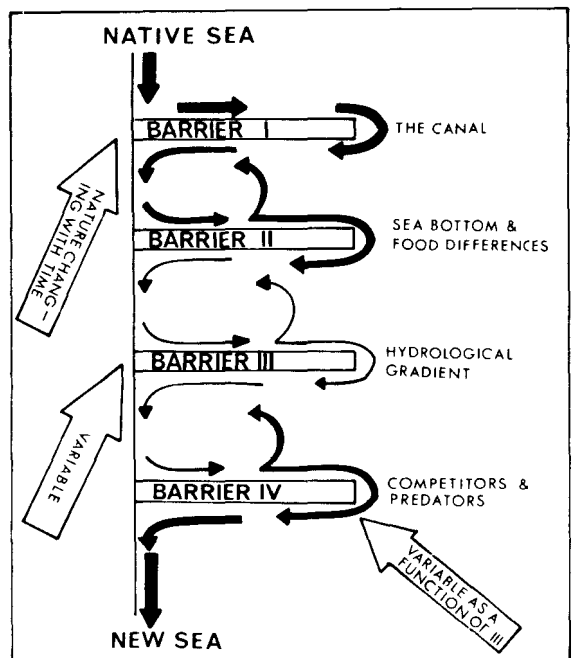


FIGURE 7.—"Barriers" on the path of a migrating species of demersal fish the last three "barriers" may occur in any order and/or overlap.

time. Animal migration through the canal may now become easier (Thorson, 1971).

The second barrier, especially for demersal species, is the difference in bottom conditions. The importance in the character of the substrate for the expansion of migrating benthic invertebrates was emphasized by Gilat (see footnote 6) and Por (1971). The type of bottom influences the type and quality of food available. Bodenheimer (1966) emphasized the negative effect which lack of food may have on fecundity. De Vlaming (1971) has shown that starvation affected the gametogenesis and gonadal regression in a goby, *Gillichthys mirabilis*. Undoubtedly, it is not enough for a bottom fish just to cross a canal. To survive and reproduce, it must find in its new habitat either the food to which it is accustomed or a food which can replace the former both quantitatively and qualitatively at all stages of its life cycle. This condition is, generally, controlled by the character of the sea bottom.

A third barrier is the hydrological gradient (if any) between both seas. A species may cross a canal, may even find an apparently suitable habitat, but all its spawn may be killed by extreme winter or summer temperatures. Also, adverse

temperature conditions may affect prespawning, reproductive processes in fish (De Vlaming, 1971), while difference or seasonal changes in salinity may affect survival of a stenohaline species.

Oren (1970) has noticed, e.g., that after the critical 1954/56 years, the minimum seawater winter temperatures over the Israel continental shelf have never returned to their values of 15°C measured prior to this period. He also found that the salinities in the same area increased since the closure of the Aswan Dam in 1964. It seems, thus, that in the long run, the hydrological gradient between the Gulf of Suez, where the temperatures and salinities are higher than in the Levant Basin (Kosswig, 1951; Oren, 1957; Ben-Tuvia, 1966) and the Mediterranean, is on the decrease.

The fourth barrier is the predators and competitors. Darwin (1859) emphasized the role of prey, predators, and competitors on the distribution range of species. Obviously, the abundance and distribution of the native predators and competitors are affected by fluctuations in the hydrological conditions. Therefore, changes in the hydrological conditions may affect establishment of the migrant species both directly and, through their competitors, indirectly.

### Human Interference May Facilitate Invasion

An invasion may succeed because of human interference in the environment. Elton (1958) has shown that such interference, especially where associated with depletion of native populations, considerably increases the vulnerability of an area to invasions. We consider commercial fisheries to be an example of an extreme interference.

### The Explosion of the Red Sea Lizardfish Population

The lizardfish, *Saurida undosquamis*, is an important component of the Egyptian trawl catches in the Gulf of Suez (Latif, 1971). The early records of lizardfish in the Suez Canal by Gruvel and Chabanaud (1937), as *S. sinaitica*, *S. tumbil*, and *S. gracilis*, may have been *S. undosquamis* (Ben-Tuvia, pers. comm.).

Fifteen years later, and 83 years after the opening of the Suez Canal, the Red Sea lizardfish appeared in the southeastern Mediterranean in suf-

ficient numbers to be described as a "rare" fish (Ben-Tuvia, 1953). But within 2 to 3 yr, it became one of the most important commercial trawl fishes forming 20% of the catch. This recalls the invasion of the sea lamprey, *Petromyzon marinus*, in the Great Lakes in North America (Elton, 1958). Although the Welland Ship Canal was opened as early as 1829, the sea lampreys were observed in Lake Erie 100 yr later. Then, within 10 yr, the lamprey population expanded rapidly and dramatically both in space and in number, causing a collapse of the lake trout fishery in Lake Michigan and Lake Huron.

The population explosion of the Red Sea lizardfish was much faster, for its 1959 all-time record landings occurred only 4 yr after its first appearance in the trawl catch as a fraction of a percent.

Although the subsequent decline in the lizardfish catch may be associated with decrease of the fishing effort (Tables 1 and 2), particularly in the northeast Mediterranean, its relatively stable proportion in the total catch indicates that an ecological balance was reached within the first 2 yr of its appearance in the commercial catch (Figures 5, 8). Subsequent annual fluctuations seem to be normal to natural populations.

TABLE 2.—Israel trawl fishery, 1948-70.

Year	Number of trawlers (activity %) <sup>1</sup>		Total landings (tons)
1945	25	(56)	508
1946	11	(73)	333
1947	12	(67)	258
1948	12	(46)	111
1949	14	(57)	430
1950	30	(54)	1,092
1951	27	(43)	929
1952	23	(49)	1,000
1953	23	(56)	1,286
1954	22	(75)	1,480
1955	27	(63)	1,518
1956	26	(60)	1,391
1957	27	(69)	1,550
1958	29	(77)	1,740
1959	27	(92)	1,952
1960	25	(69)	1,274
1961	19	(70)	992
1962	18	(75)	830
1963	17	(74)	706
1964	15	(76)	615
1965	18	(70)	761
1966	18	(77)	638
1967	16	(87)	741
1968	16	(80)	926
1969	16	(91)	1,028
1970	19	(82)	930

<sup>1</sup>Activity index (100%):  
below 150 hp 210 days at sea per trawler.  
over 150 hp 230 days at sea per trawler.

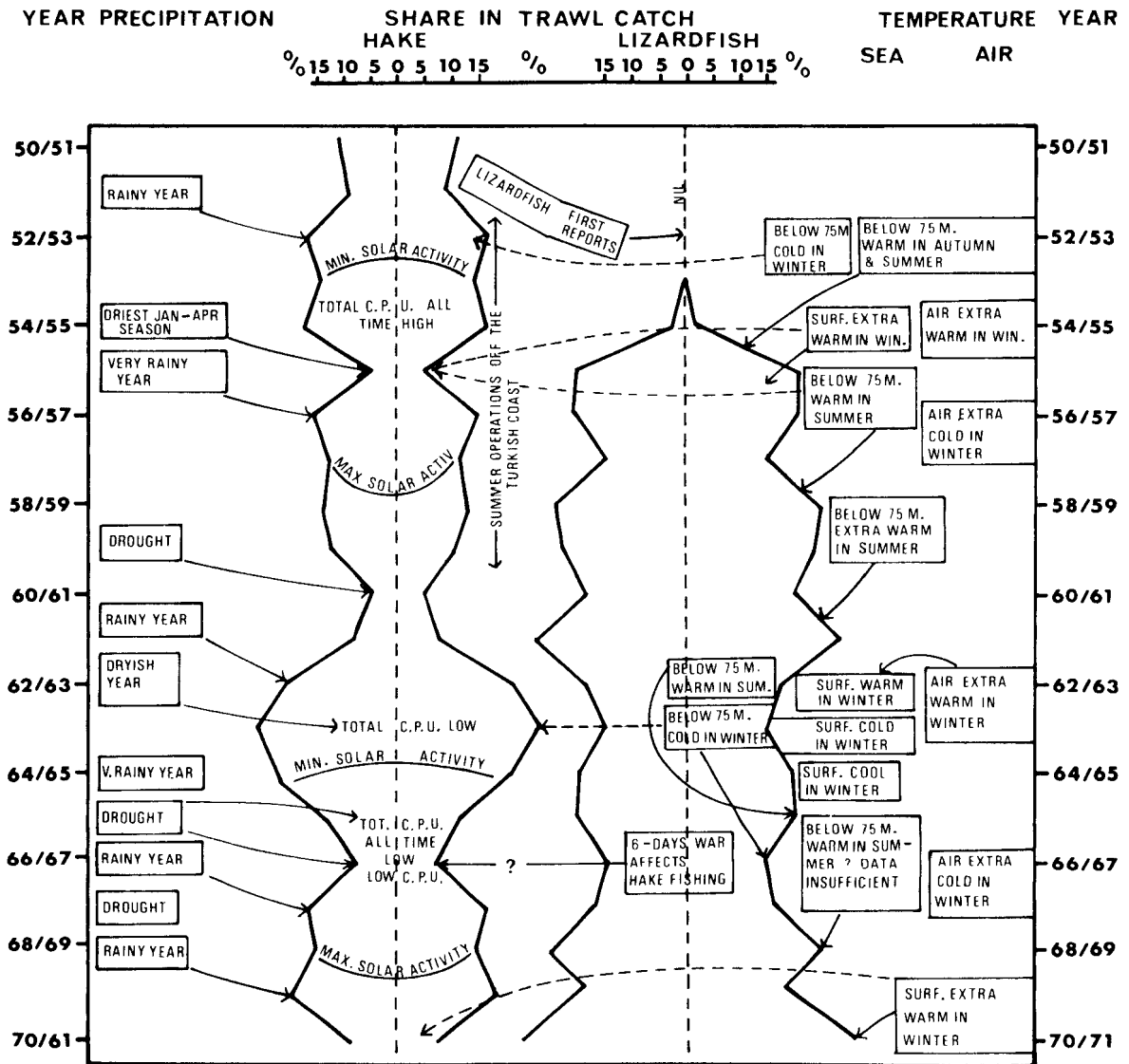


FIGURE 8.—Changes of the proportion of the hake and the Red Sea lizardfish in the Israel trawl landings and their relationship with environmental conditions, 1950-71.

Hence, in the case of the lizardfish, the population-growth logistic curve (Bodenheimer, 1966) would have been extremely steep in its central part with extremely sharp flexes between the first and the central sections and, again, between the central and the third sections of the curve. It can be, therefore, speculated that this invasion and expansion were not only a product of a "normal" population growth but were also aided by additional factors.

### The Role of Environmental Factors

The sudden buildup of the Red Sea lizardfish population which occurred between 1954 and 1956 was accomplished by a series of unusual phenomena: 1) unusually high temperatures, both of air and water (Ben-Yami, 1955; Oren, 1957), especially in winter (Figures 1, 2, 3); 2) the extremely dry January-April season of 1955 (Figure 4), as well as a very pronounced absence of winter

gales of anticyclonic depression origin, during the same winter (Ben-Yami, 1955); 3) the hake made a very poor appearance in the 1955/56 Israel trawl catches (Figures 5, 8), decreasing to approximately 40% of its 20 yr average (Figures 5, 8) in the catch and to approximately 42% of its 20 yr average (Figure 5) in its catch per fishing day. Since then, such low catches of the hake only occurred in 1960/61 and in 1966/67. In all three cases, the drop in the hake catches seems to be associated with drought: it followed the January–April drought in 1955, in 1959/60 and 1966/67 it followed a drought in the preceding winter (Figure 8).

### Trawl Fishery's Rapid Development

The rapid intensification of the Israel trawl fishery 1949-54 (Table 2) was probably another important factor contributing to the expansion of the Red Sea lizardfish. The landings, which before 1940 were 100 to 500 tons, rose to approximately 1,000 tons/year during 1950–52 and to almost 1,500 tons in 1954, when the first commercial catches of the lizardfish were taken.

Before 1950, the Israeli trawlers did not fish in waters deeper than 50 to 60 fm. Since 1950, deepwater trawling operations have been carried out, and hence there has been considerable exploitation of the hake resources (Ben-Yami, 1971).

### DISCUSSION AND CONCLUSIONS

The set of conditions which prevailed just before and during the explosion of the Red Sea lizardfish population and which, apparently, facilitated this explosion included:

1. "Preparation" of the area due to the intensification of the trawling fishery by the factor of 3-4 (Table 2);
2. Water temperature conditions which contributed to good survival of several strong year classes of lizardfish;
3. A combination of climatic (drought) and water temperature conditions which caused the withdrawal of the hake from most of the trawling grounds, leaving ample space for the spread of the lizardfish.

It is possible that the population of the Red Sea lizardfish in the Levant Basin has been and, without these conditions, might have remained "dormant" and suppressed by its competitors and by unfavorable environmental conditions. It may

have been still waiting for its opportunity to expand.

The fluctuation in the abiotic conditions, subsequent to the lizardfish explosion years, seems to be correlated with the fluctuations in the catches of both the lizardfish and the hake, though with an "anomaly" in 1961-63 when, in spite of two consecutive warm winters, the proportion of hake increased in comparison to the lizardfish. Here, e.g., the abundant rains of 1961-62, or other factors might have intervened (Figure 8).

The hake is much more sensitive to the fluctuations of physical conditions than the lizardfish, as may be seen from the shape of the respective columns in Figure 8. The declines in the hake catches indicate either recessions in the population or a geographical retreat from the usual fishing grounds, probably into deeper and cooler waters, or a combination of both.

An interesting feature of the fluctuation of the hake proportion in catches is that so far they are in phase with those of the solar activity index (Figure 8), though this correlation may be purely incidental.

The interrelations discussed in this paper are very complex. Different and, perhaps, even variable time lags have to be employed to correlate abiotic, biotic-natural, and man-activated (fisheries) factors. A study for further pursuit along this line will require the application of computer technique. Unquestionably, a good opportunity for studying the influence of environmental conditions on the relationship of competing migrant and native species was lost when data on the *Mullus-Upeneus* and Red Sea Barracuda–Atlantic Barracuda proportion in catches were not collected during the past years. Such studies should be undertaken in the future.

An examination of the available statistical data (Sarid, 1951-71) could not establish any significant influence of the appearance of the Red Sea lizardfish in the total trawl catches on the landings, catch per unit effort, or returns of the trawl fishery. Undoubtedly, the lizardfish is not just an additional inhabitant, and its invasion did not enrich the existing ecosystem in terms of biomass. It occurs in the catches at the expense of other fish, partly its competitors, such as the hake, and partly its prey, such as the yellow-striped goatfish, red mullet, etc.

The proportion of the lizardfish in the trawl catches has never, after its 1954-56 invasion, been less than 13%, although there have been several

cold winters since (Figures 2, 3, 8). This, besides indicating that the Red Sea lizardfish is fairly eurythermic, may also support Kosswig's (1972)<sup>13</sup> suggestion of the role of the modifiability of species in new environments. It is quite probable that the Mediterranean stock of the Red Sea lizardfish today is better adapted to the local environmental conditions than it was 20 yr ago.

The Red Sea lizardfish proved vigorous enough to establish itself in a niche in a habitat occupied by other species; it is euryecous enough to withstand fluctuations in environmental conditions; and, barring an ecological disaster, it is here to stay.

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