Females held in the bottom cage or in the laboratory tanks were subject to less ambient light, more stable temperatures, and water below the photosynthetic zone. The laboratory water system utilizes water pumped from an area 2 m above the sea floor, thereby approximating the water available to the bottom caged prawns. Previous work has shown that juvenile and yearling prawns are sensitive to rapidly fluctuating water temperature, light, and plankton blooms (Rensel and Prentice[1]).

A second spawning was recorded for 85.4% of the surviving females. The average carapace length of these spawners was 39.2 mm (SD = 1.31). Eggs developed normally, producing viable larvae, but the fecundity was low, ranging from 10 to 1,000 eggs. The fecundity of wild bred stocks is 2,000–5,000 eggs per female. The reduced fecundity in the female prawns spawning for the second time may be due to nutritional or environmental factors. However, in some instances the female prawns were observed actively removing eggs from their own abdomens, using the second pereiopod. In other cases, we observed egg losses during the holding period due to abrasion on the nets and tanks.

Multiple breeding and spawning are common in other families of caridean shrimps, but among the Pandalidae only *P. montagui* Leach in the northeastern Atlantic Ocean has been known to spawn for two consecutive years (Allen 1963). This study shows that female spot prawns can also successfully breed, spawn, and hatch eggs for a second time. This is important to both the aquaculturist and the field biologist. If multiple breeding also takes place in wild populations, then estimates of year–class recruitment based on single spawning populations are in error.

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EFFECT OF DISSOLVED OXYGEN CONCENTRATION AND SALINITY ON SWIMMING SPEED OF TWO SPECIES OF TUNAS

Studies on captive skipjack tuna, *Katsuwonus pelamis*, have determined three physiological parameters that may operate to delimit oceanic distribution of this fish. If 1) a lower temperature limit of 18°C, 2) a size-dependent upper temperature limit, and 3) a lower oxygen limit of 5 ppm are mapped onto the temperature and oxygen levels of the central Pacific area, the resulting model is consistent with many of the peculiar features of the geographical distribution of the skipjack tuna (Barkley et al.[1]). In particular, the exclusion of adult skipjack tuna from warm, oxygen-poor waters of the eastern tropical Pacific Ocean is explained.

But the physiological parameters used in the model were either speculative—upper temperature limits—or based upon acute and stressful experimental conditions—lower oxygen and temperature limits. Gooding and Neill[2] determined the lower oxygen limit by introducing tunas into a small tank (1.8 × 2.4 × 0.6 m oval) containing

[1]Barkley, R. A., W. H. Neill, and R. M. Gooding. Skipjack tuna habitat based on temperature and oxygen requirements. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.–1 Oct. 1975.)
[2]Gooding, R. M., and W. H. Neill. Respiration rates and reactions to low oxygen concentrations in skipjack tuna, *Katsuwonus pelamis*. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

seawater at a given level of oxygen saturation. Swimming speed and survival time were measured. They found that survival time and swimming speed were independent of oxygen levels in excess of 4 ppm; below 4 ppm survival time was directly and swimming speed inversely proportional to dissolved oxygen amounts. So apparently 4 ppm is close to the incipient lower lethal limit for skipjack tuna under the given experimental conditions. For modeling distribution limits, Barkley et al. (see footnote 1) used a more conservative figure of 5 ppm.

However, a physiological limit of 4 or 5 ppm is not necessarily a behavioral limit; if the limit is approached slowly under natural and otherwise unstressful conditions, can a fish adaptively respond? Whitmore et al. (1960) found that coho salmon, *Oncorhynchus kisutch,* avoided water of lowered oxygen levels yet which produced no respiratory distress. In contrast, kawakawa, *Euthynnus affinis,* a species closely related to skipjack tuna, tolerated 2-ppm water for short periods in order to get food (Chang and Dizon[3]).

In the present experiment, I tested the responses of free-swimming tunas—both skipjack tuna and yellowfin tuna, *Thunnus albacares*— encountering slowly changing oxygen levels. The rate of change was comparable with that which a tuna might encounter in nature. Yellowfin tuna were tested for comparison because they are abundant in the same areas of the eastern tropical Pacific avoided by large skipjack tuna. Finally, salinity fronts have been suggested as a factor determining distribution, so responses to decreasing salinity levels were also examined.

Materials and Methods

Eight skipjack tuna and three yellowfin tuna were tested with decreasing oxygen levels, and three skipjack tuna, and one yellowfin tuna were tested with decreasing salinity levels. Fish were chosen from stocks at the Kewalo Research Facility of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii. Tuna stocks for this experiment were kept in outdoor tanks (7.3 m diameter × 1.2 m deep) until used; they were then removed by angling

[3]Chang, R. K. C., and A. E. Dizon. Low oxygen levels as barriers to voluntary movements of tunas. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.–1 Oct. 1975.)

with a barbless hook and transferred to the swim chamber in a plastic bag partially filled with water. This is a good transfer technique since fish on occasion have fed immediately after transfer.

The responses of tunas to decreasing oxygen and salinity levels were examined in a tank system consisting of a swim chamber equipped with photocells for monitoring and recording fish behavior. (For details see Dizon et al. 1977.) The swim chamber was a 6.1 m diameter × 0.61 m deep fiber glass tank fitted with a concentric inner wall so the fish was constrained to swim in a 0.75-m channel around the periphery. Six laps equaled 100 m. Water (24°C) was introduced and removed from the swim channel through two pairs of concentric rings of polyvinyl chloride pipe. Entering (or exiting) water divided equally into two inflow (or outflow) pipes, each flowing countercurrent to the other to provide minimum oxygen or salinity asymmetry and horizontal transport of water within the swim channel. Water was recirculated through an outside circuit at 1,136 liters/min to insure thorough mixing of any introduced new water. New seawater was added to the tank at 38 liters/min.

Oxygen was reduced in the tank by replacing the 38 liters/min new seawater with 38 liters/min anoxic seawater obtained at our well head before aeration and introduced into the intake of the 1,136 liters/min recirculation pump. Oxygen decreased approximately exponentially within the swim chamber—0.06 ppm/min after 30 min and 0.03 ppm/min after 60 min. Salinity levels in the swim chamber were reduced by introducing aerated freshwater (38 liters/min) into the pump intake. Salinity decreased exponentially—0.07‰/min after 30 min and 0.03‰/min after 60 min.

Passage of the fish was sensed at four photocell stations (six photocells/station) at 90° intervals around the periphery of the swim channel. Information from the photocells was translated into swimming speed (minutes per lap), direction (clockwise or counterclockwise), and frequency of reversals or swimming direction by digital logic equipment and printed on adding machine tape.

Procedures were quite simple; tuna (starved for 1 day) were moved into the tank and allowed 100 min to habituate; swimming speeds were continuously recorded to provide baseline data to compare with behavior during periods of changing oxygen or salinity. After 100 min, a test was started and behavior was recorded as salinity or oxygen decreased. Oxygen and salinity levels were allowed

to reach 2 ppm and 29‰, respectively. After reaching these levels (about 200 min), test water was shut down and normal seawater restored. The following morning fish were removed, weighed, and measured, and survivors were returned to holding tanks. Oxygen and salinity levels were monitored by oxygen meter and salinograph; samples were taken periodically for laboratory analysis to verify the instruments.

Results and Discussion

Behavioral responses to decreasing levels of salinity were unremarkable; Table 1 summarizes results from three skipjack tuna and one yellowfin tuna. No consistent swimming speed changes were observed during periods when salinity decreased from about 34‰ to 29‰. Although sample size is small, these tunas did not make any dramatic response to salinity changes of magnitudes expected within their normal habitat.

Figure 1 illustrates typical results from tunas encountering slowly changing oxygen concentration. At or about 4 ppm, skipjack tuna (Figure 1a) demonstrated an abrupt increase in swimming speed. In most fish tested, speed increased to over 2 lengths/s. Yellowfin tuna, in contrast, showed no alteration in swimming speed as oxygen levels decreased (Figure 1b).

Figure 2 summarizes the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Individual points plotted are median swimming speeds for the eight skipjack tuna grouped by: 1) before treatment and 2) 1-ppm dissolved oxygen intervals both decreasing and increasing, i.e., 6–5, 5–4, 4–3, 3–2, and 2–3, 3–4, 4–5, 5–6. Number of swimming speeds sampled ranged from under 5 to over 100 depending on the number of laps swum during each interval. Heavy line connects the grand median of each interval. Simi-
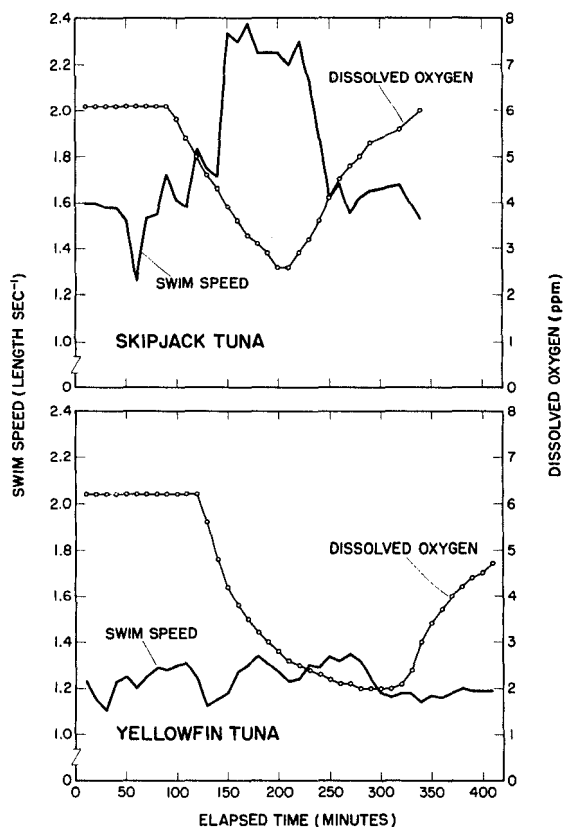

FIGURE 1.—Effect of dissolved oxygen level on swim speed in two species of tunas. Swim speeds are median values sampled for 10-min periods.

lar data for each yellowfin tuna (decreasing oxygen intervals only) are included for comparison.

Not all of the skipjack tuna survived the treatment; three of the eight died when oxygen levels dropped below about 2.5 ppm. Survival times for skipjack tuna under conditions of low oxygen are as follows: in excess of 240 min at 4 ppm, 59 min at 3 ppm, and 18 min at 2 ppm (Gooding and Neill see footnote 2). My data are consistent with this resistance–time distribution, and both studies support the Barkley et al. (see footnote 1) hypothesis that there does exist a low oxygen level that limits the observed oceanic distribution of skipjack tuna.

Yellowfin tuna are not apparently stressed during the exposures to the low oxygen water employed. In separate tests done after the exposures to decreasing oxygen, two additional yellowfin tuna survived and made no overt locomotory changes when introduced directly into water

TABLE 1.—Effect of decreasing salinity on mean swimming speed in tunas.

| Item	n	x̄ (length/s)	SD
Skipjack tuna 1 (38.3 cm, 925 g)			
Before salinity change	28	2.10	0.40
During salinity change	22	1.82	0.40
Skipjack tuna 2 (37.7 cm, 882 g)			
Before salinity change	44	2.03	0.26
During salinity change	12	2.37	0.19
Skipjack tuna 3 (42.0 cm, 1,352 g)			
Before salinity change	30	1.21	0.07
During salinity change	15	1.16	0.06
Yellowfin tuna 1 (45.3 cm, 1,491 g)			
Before salinity change	39	1.54	0.30
During salinity change	31	1.81	0.26
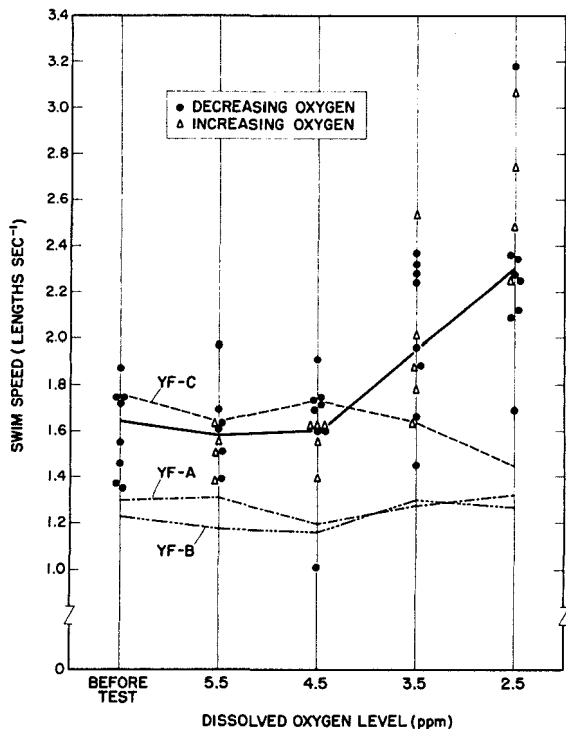
FIGURE 2.—Summary of data from the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Dots — decreasing oxygen levels, median swim speeds grouped by 1-ppm intervals and "before" test observations. Open triangles — increasing oxygen levels, median swim speeds grouped by 1-ppm intervals. Solid line — grand median for eight skipjack tuna. Broken lines — medians for each of the three yellowfin tuna, decreasing oxygen levels only.

containing 1.4 and 1.6 ppm oxygen. They survived a 200-min exposure and a 100-min recovery period. By way of contrast, brook trout, *Salvelinus fontinalis,* LD_{50}'s for 1.5 ppm and 1.4 ppm were 300 and 100 min, respectively (Shepard 1955). The brook trout and the yellowfin tuna were swimming at about the same speeds, 1.0–1.5 lengths/s. Although conditions of the two experiments are in no way similar, these data do imply that yellowfin tuna are at least as low oxygen tolerant as brook trout. The higher energy requirements (larger fish, warmer water) of yellowfin tuna allow this conclusion. Perhaps if oxygen levels dropped low enough in my tank (1.4 ppm is about the lowest that could be achieved), an increase in speed similar to that in skipjack tuna would have been observed.

Increased swimming speed should function either to remove the fish from suboptimal areas (if

coupled with some directive stimuli) or to provide more water to the gills—tunas are ram ventilators. Within the skipjack tuna habitat, water deficient in oxygen is found within and below the thermocline (Barkley et al. see footnote 1). Appropriate behavior would be to swim up and out of the low-oxygen water. Even without a change in direction, angle of attack of pectoral fins, or body attitude, increased swimming speed alone will cause a tuna to rise due to increased lift (Magnuson 1973).

Faster swimming speeds do not seem to be a response to increase ram ventilation (open mouth swimming). Increased flow over the gills providing more oxygen delivery is offset by increased respiratory demands imposed by faster swimming. Under conditions of saturated seawater (7.2 mg O_2/liter), 15% head loss along the respiratory flow path (Brown and Muir 1970), a conservative oxygen utilization factor of 75% (Stevens 1972), and a 1 cm² mouth gape (Brown and Muir 1970), oxygen is delivered to the gills at the rate represented by the middle broken line (Figure 3). This, of course, also increases as swimming speed increases. Respiratory demand (solid black line) and oxygen delivery intersect at two points: the lower is at the minimum swimming speed that can still furnish sufficient oxygen for an animal in an almost basal state and the upper is a point at which exponentially increasing respiratory demand again exceeds linearly increasing oxygen delivery.

The latter would seem to be maximum sustained swimming speed; anaerobic metabolism would be necessary at speeds above. However, neither function (anaerobic or aerobic) may be correctly extrapolated to the faster swimming speeds. Respiratory demand might well be less at higher speeds if swimming efficiency increases.

Yet, if dissolved oxygen concentration drops to 4 ppm, increase in swimming speed is an inefficient way to make up the deficit (lower broken line). But, increase gape to 2 cm² (I am assuming for argument's sake that this doubles ventilation volume) restores the amount of oxygen delivered (upper broken line). In summary, I suspect that increased swimming speed of skipjack tuna encountering oxygen-deficient water is not due to ram ventilation needs but rather is a behavioral response to remove an animal from a suboptimal area. Considering the relative expense of faster swimming in terms of oxygen needs, the modest increases in swimming speeds observed are probably very adaptive in that they should cause a
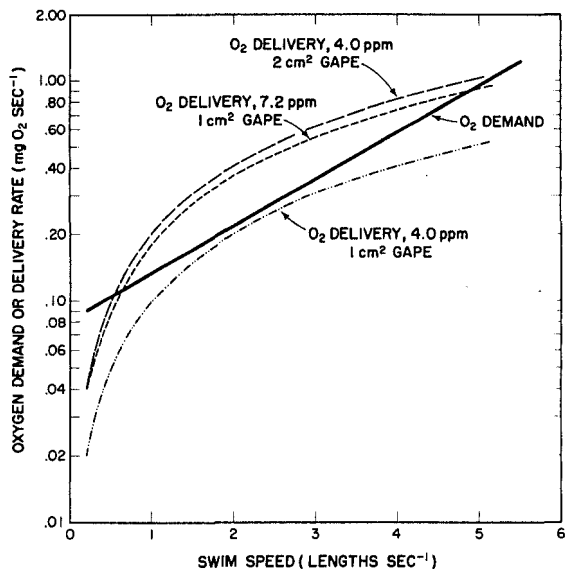
FIGURE 3.—Respiratory demand (Gooding and Neill see footnote 2) versus respiratory supply (Brown and Muir 1970; Stevens 1972) as a function of swimming speed in a 40-cm, 1.4-kg skipjack tuna. Respiratory demand increases geometrically while respiratory supply increases arithmetically with increasing swimming speed. When oxygen concentration decreases it is more efficient to increase ram ventilation by increasing gape rather than simply swimming faster.

fairly rapid rise in the water column at a relatively low energetic cost. Yellowfin tuna, in contrast, are just not stressed at the levels of saturation employed in our experiments. Yellowfin tuna should be able to occur in the anoxic water in or below the thermocline and since in the eastern central Pacific Ocean anoxic, cool waters are as inhospitable as the upper too warm waters, skipjack tuna may find no suitable habitat.

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A NONLETHAL LAVAGE DEVICE FOR SAMPLING STOMACH CONTENTS OF SMALL MARINE MAMMALS

Historically, the only expedient and successful method for determining the species upon which marine mammals feed has been to kill the animal, remove its stomach, and examine the contents in the laboratory (e.g., Wilke and Nicholson 1958; Tautsumi et al. 1961; Shomura and Hida 1965; Fiscus and Baines 1966; Fitch and Brownell 1968; Imler and Sarber 1947). This method, however, does not always work. For example, when actively feeding marine mammals are harpooned or shot, they sometimes regurgitate most or all of their food. While regurgitation by live captured marine mammals is possible, it does not appear to be a significant problem. Of the last 10 cetaceans that I have captured alive and later released unharmed, none has regurgitated during the capturing, handling, or releasing process. Although some researchers have reported on stomach samples from stranded marine mammals (e.g., Houck 1961; Fitch and Brownell 1968), these samples may not be representative of feeding habits of active healthy organisms.

Passage of the Marine Mammal Act in 1972 has made it necessary to develop techniques beside killing if we are to continue certain types of marine mammal research. A useful tool for determining feeding habits of delphinids and certain small pinnipeds would be a portable stomach pump device capable of being used in the field. To be effective, this device must be capable of removing small identifiable bits of food such as otoliths, scales, preopercular bones, squid beaks, or other