Temporal variation in growth of yellowfin tuna (*Thunnus albacares*) larvae in the Panama Bight, 1990–97

Jeanne B. Wexler (contact author)[1]
Seinen Chow[2]
Toshie Wakabayashi[3]
Kenji Nohara[3]
Daniel Margulies[1]

Email address for J. B. Wexler: jwexler@iattc.org

[1] Inter-American Tropical Tuna Commission
8604 La Jolla Shores Drive
La Jolla, California 92037-1508

[2] National Research Institute of Fisheries Science Nagai
6-31-1 Yokosuka
Kanagawa 283-0316 Japan

[3] National Research Institute of Far Seas Fisheries
5-7-1 Shimizu-Orido
Shizuoka 424-8633 Japan

Abstract—Tuna larvae (at flexion, postflexion, and transformation stages) were collected by dip net and light traps at night in the northwestern Panama Bight during the season of reduced upwelling (June–September) of 1990, 1991, 1992, and 1997. The larvae were identified as yellowfin tuna (*Thunnus albacares*) by mtDNA analysis. Ichthyoplankton data from bongo and Tucker trawl tows were used to examine the potential prey abundance in relation to the mean size-at-age and growth rates of the yellowfin tuna larvae and their otoliths. The most rapid growth rates occurred during June 1990 when plankton volumes were at their highest levels. The lowest plankton volumes coincided with the lowest growth rates and mean sizes-at-age during the August–September 1991 period. High densities of larval fish were prevalent in the ichthyoplankton tows during the 1991 period; therefore intra- and interspecific competition for limited food resources may have been the cause of slower growth (density-dependent growth) in yellowfin tuna larvae The highest mean sea-surface temperature and the lowest mean wind stress occurred during an El Niño-Southern Oscillation (ENSO) event during the 1997 period. There appeared to be no clear association between these environmental factors and larval growth rates, but the higher temperatures may have caused an increase in the short-term growth of otoliths in relation to larval fish size.

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Yellowfin tuna (*Thunnus albacares*) larvae inhabit the mixed layer of all tropical and subtropical oceans of the world (Ueyanagi, 1969; Nishikawa et al., 1985). When recruited to the commercial fishery, yellowfin tuna are one of the most important tuna species worldwide (Collette and Nauen, 1983; FAO, 2004). Near-daily spawning of yellowfin tuna, and the subsequent dispersal of fertilized eggs, appears to be largely dependent on the occurrence of surface water temperatures equal to or greater than 24°C (Schaefer, 1998). In the eastern Pacific Ocean (EPO), yellowfin tuna spawn continuously between 0° and 20°N (Schaefer, 2001). Despite widespread spawning of yellowfin tuna throughout the EPO, the larvae are patchy in distribution (Ahlstrom, 1971), and relatively large numbers have been collected only near islands (Graves et al., 1988; this study) and near shore (González Armas, 2002).

The larvae of *Thunnus* are difficult to identify by meristic, morphological, or pigmentation characteristics (Matsumoto et al., 1972; Potthoff, 1974; Richards et al., 1990; Lang et al., 1994). In the EPO, the late-larval and early-juvenile stages of yellowfin and bigeye (*T. obesus*) tuna co-exist and cannot be differentiated by these conventional methods. However, allozyme (Graves, et al., 1988) and recent molecular (Takeyama et al., 2001; Chow et al., 2003) analyses have made it feasible to identify larvae of these two species that inhabit the EPO.

The growth dynamics of yellowfin tuna during early life stages may have a profound effect on cohort strength (Houde, 1987), but growth rates have not been described for the larvae in the Pacific Ocean. Larval and juvenile stage durations and corresponding growth rates (Houde, 1989), starvation rates (Margulies, 1993), and larval transport and predation (Grimes, 2001) may be strongly influenced by biological and physical processes that would affect prerecruit survival in yellowfin tuna. Standing stocks of phytoplankton and zooplankton in the EPO, where yellowfin tuna larvae are found are seasonally variable (Blackburn et al., 1970; Owen and Zeitschel, 1970; Lauth and Olson, 1996; González Armas, 2002) and influenced by interannual events such as El Niño-Southern Oscillation (ENSO) conditions (Dessier and Donguy, 1987; Fiedler, 1992; Chavez et al., 1999; Strutton and Chavez, 2000). In the northwestern Panama Bight of the EPO, nearshore ichthyoplankton surveys (from 1989 to 1993)

Table 1

Collections of yellowfin tuna larvae by night-lighting (NL) and light traps (LT) near Frailes del Sur in the northwestern Panama Bight, 1990–1997.

Sampling period	Number of sampling dates	Number of larvae collected	Number used for age and growth analyses	Number used for ( ) and identified as *T. albacares* by PCR-RFLP analysis	Age range (days)	Standard length range (mm)
21–26 June 1990	3	97 (NL)	25	(5) 1	8–18	6.2–19.6
5–25 July 1991	5	13 (NL) 9 (LT)	13	(13) 10	11–15	9.1–12.7
4–7 September 1991	2	126 (NL)	43	(34) 26	12–20	7.1–12.4
24 June–3 July 1992	3	47 (NL)	22	(34) 19	10–14	7.6–12.0
7 August 1997	1	98 (NL)	69	(71) 69	11–18	8.7–14.5

(IATTC[1]; IATTC[2]; Lauth and Olson, 1996; Owen[3]) and experiments with captured scombrid larvae (from 1986 to 1997) at the Achotines Laboratory of the Inter-American Tropical Tuna Commission (IATTC) (Olson and Scholey, 1990; Margulies, 1993; Scholey, 1993; Wexler, 1993) have provided an opportunity to explore factors controlling prerecruit growth and survival of scombrids. These small- and fine-scale studies may provide some understanding of the recruitment variability of yellowfin tuna in the Panama Bight, considering that yellowfin tuna exhibit limited, small-scale movements within the EPO (Schaefer, 1991; Wild, 1994) and that processes important to recruitment probably occur at small scales (Fortier and Leggett, 1985).

The Panama Bight is characterized by distinct seasonal and interannual variations in atmospheric and oceanic conditions (Wooster, 1959; Smayda, 1963, 1966; Forsbergh, 1963, 1969). The climatological and physical oceanographic properties that occur within the Panama Bight are determined by the north-south seasonal movement of the northeast trade winds of the Atlantic Ocean, the equatorial calm belt (i.e., the doldrums), the southeast trade winds of the Pacific Ocean, and the convergence of these trade wind systems within the doldrums (i.e., the intertropical convergence zone, ITCZ) (Smayda, 1966). From January through April, the ITCZ is displaced to the south and strong northerly trade winds create a dry season and produce local upwelling. From about May through December, the ITCZ is displaced to the north and the Panama Bight is dominated by southeast trade winds and a rainy season characterized by reduced upwelling, higher sea-surface temperatures (SSTs), lower ocean salinities, and a deeper thermocline and mixed layer (Lauth and Olson, 1996). The growth and subsequent survival of yellowfin tuna larvae that occur during the reduced upwelling season may be regulated more by the spatial patchiness of prey organisms coincident with lower plankton volumes (Owen, 1989). ENSO events could further affect the seasonal availability of nutrients and food organisms during this period (Barber and Chavez, 1986; Dessier and Donguy, 1987; Fiedler, 1992; Chavez et al., 1999). A mild ENSO event occurred during our sampling periods in 1991–92 (Barber et al., 1996) and a strong event occurred in late 1997 (Chavez et al., 1999; Strutton and Chavez, 2000; Glynn et al., 2001).

The objectives of this study were 1) to identify the species of *Thunnus* sampled in the northwestern Panama Bight by molecular analysis, 2) to determine ages and compare the size-at-age data of yellowfin tuna larvae collected during the periods of reduced upwelling of 1990, 1991, 1992, and 1997, and 3) to explore relationships between the temporal variation in growth rates and measured levels of plankton and physical processes in the Panama Bight.

Materials and methods

Larval fish collections

Fish larvae were collected in the northwestern Panama Bight (Fig. 1) during the seasons of reduced upwelling in June 1990, July and September 1991, June and July 1992, and August 1997 (Table 1). Most of the larvae were collected with a dipnet just below the ocean surface after they were attracted with an underwater light at night (night-lighting, NL) (Olson and Scholey, 1990) near Frailes del Sur in the vicinity of the 100- and 200-meter isobaths. Larvae were also collected in this area in July 1991 by a light trap (LT) (design described in Thorrold,

[1] IATTC (Inter-American Tropical Tuna Commission). 1992. Annual report of the Inter-American Tropical Tuna Commission 1990, 261 p. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

[2] IATTC (Inter-American Tropical Tuna Commission). 1992. Annual report of the Inter-American Tropical Tuna Commission 1991, 271 p. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

[3] Owen, R. W. 1997. Oceanographic atlas of habitats of larval tunas in the Pacific Ocean off the Azuero Peninsula, Panama, 32 p. Inter-American Tropical Tuna Commission Data Report 9. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

1993) deployed near the surface. All larvae were fixed in 95% ethyl alcohol shortly after capture, except for some that were caught alive and used in laboratory experiments. Fish used in laboratory experiments were not used for the age and growth analyses. SSTs were recorded with a bucket thermometer, and the salinity of a sample of water taken just below the surface was measured with a handheld salinometer. Visual observations of environmental conditions (e.g., wind, currents, and weather) were recorded at the time of sampling.

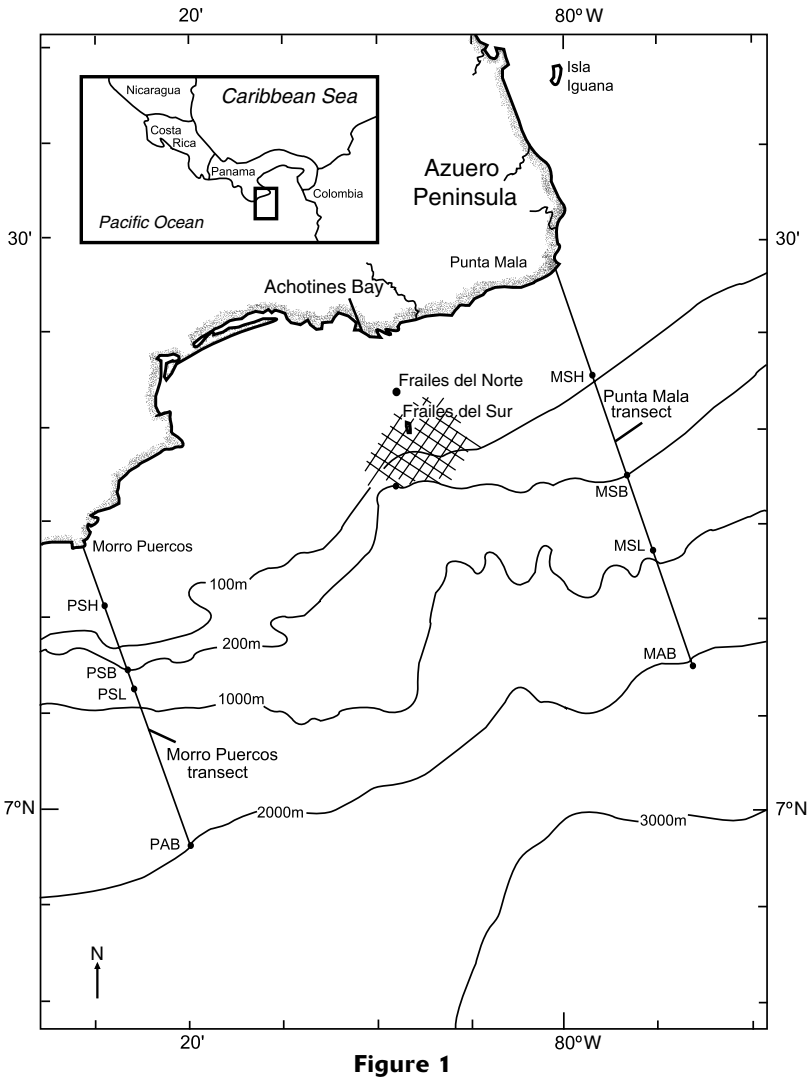

Figure 1

Locations where yellowfin tuna (*Thunnus albacares*) larvae were collected with an underwater light at night (cross hatched; from 1990–92 and 1997) and where ichthyoplankton sampling occurred (during 1990–92) near the Achotines Laboratory, on the Azuero Peninsula of the northwestern Panama Bight. Ichthyoplankton sampling stations along the Punta Mala and Morro Puercos transects are the following: Mala abyss (MAB), Mala slope (MSL), Mala shelf break (MSB), Mala shelf (MSH), Puercos abyss (PAB), Puercos slope (PSL), Puercos shelf break (PSB), Puercos shelf (PSH).

Laboratory procedures and analyses

Larvae of the genus *Thunnus* were sorted from other scombrid larvae by the morphological features and meristics described in Nishikawa and Rimmer (1987) and Ambrose (1996). The standard length (SL) of each larva was measured in distilled water before the sagittal otoliths were removed for aging and before the remaining tissue of each individual was placed in 95% ethyl alcohol for species identification. The sagittae were removed, cleaned of tissue with chlorine bleach, rinsed in distilled water, dried, and embedded distal side up with Eukitt (O. Kindler, Freiberg, Germany) mounting medium on a glass slide. The diameter along the longest axis of each sagitta was measured with an ocular micrometer and light microscope. The sagittae were polished at the surface until the increments were clearly visible with transmitted light at a magnification of 480 or 720×. Daily increments (previously validated in Wexler et al., 2001) of the left and right sagittae were counted "blindly" (i.e., repeated counts were made without prior knowledge of the previous counts) by the first author until the same number of increments were counted at least three times in one of the sagittae. The number of increments in the sagitta that was more clearly read (which usually resulted in a higher count) was used as a direct estimate of age for that fish.

The temporal variation in growth was examined by comparing the size-at-age data of the larvae and their otoliths among collection periods through analysis of covariance (ANCOVA) and a multiple range comparison test (Tukey HSD) (XLSTAT vers. 7.5.2, Addinsoft USA, New York, NY) (α=0.05).

DNA analysis and species identification

The flanking region between ATPase 6 and cytochrome oxidase subunit I (COI) genes of mtDNA was amplified by using the polymerase chain reaction (PCR), and restriction fragment length polymorphism (RFLP) patterns were used to identify the species of *Thunnus* larvae according to protocols of Takeyama et al. (2001) and Chow et al. (2003). Albacore (*T. alalunga*), yellowfin, and bigeye tunas in the Pacific Ocean can be identified by the diagnostic restriction profile of *Mse* I digestion (Chow and Inoue, 1993), and this enzyme assay was used to identify the species of larvae collected in 1990–92. Chow et al. (2000) found, however, that many specimens of bigeye tuna in the Atlantic Ocean shared the same restriction profile with yellowfin tuna; this also occurred in the Pacific Ocean, but at a much lower frequency (1 out of 144 individuals examined). Takeyama et al.

Table 2

Maximum distances traveled for each collection group of yellowfin tuna larvae recruited to the sampling area based on back-calculated spawning dates, the period of time over which the larvae were exposed to environmental conditions during their life history, and an average, maximum current speed and direction for the Panama Bight region (Fiedler, 2002). The average latitudinal and longitudinal degrees traveled were used to estimate an area occupied by larvae of all collection groups. The mean sea surface temperature (SST) is based on monthly averages within 1- by 1.5-degree ares for each collection group period within the estimated area.

Collection group	First spawn date	Last sample date	Monthly mean SST (SE) and ranges (°C)	Time period exposed to ambient SST (days)	Number of days feeding	Maximum meters traveled @ .25 m/sec	Maximum nautical miles traveled	Degrees
I	6/6/1990	6/26/1990	27.84 (0.090 26.4–28.7	20	17	432,000	233	3.89
II	6/19/1991	7/25/1991	27.90 (0.063) 26.6–28.7	36	33	777,600	420	7.00
III	8/14/1991	9/7/1991	27.60 (0.059) 26.5–28.4	24	21	518,400	280	4.66
IV	6/9/1992	7/3/1992	28.00 (0.066) 26.4–29.0	24	21	518,400	280	4.66
V	7/19/1997	8/7/1997	29.10 (0.046) 28.3–30.0	19	16	410,400	222	3.69
							mean degrees	4.78

(2001) found another restriction enzyme (*Tsp* 509I) that was diagnostic for bigeye tuna regardless of where the specimens came from. Therefore, in addition to using *Mse* I digestion, *Tsp* 509I was also used for all individuals collected in 1997.

Back-calculated dates

Spawning dates were back-calculated for each larva by subtracting the number of otolith increments counted from the date the larva was collected. An additional day was also subtracted because the first increment in yellowfin tuna is present at hatching approximately 20 hours after fertilization (senior author, personal commun.) and the second increment does not form until the third day after fertilization (approximately two days after hatching); increments are formed daily thereafter (Wexler et al., 2001). During the reduced upwelling season when SSTs are warmer, first feeding of the larvae occurs at first light, approximately three days after hatching (Margulies et al., in press) when, on average, three increments are present in the sagittae. Therefore, three days were subtracted from the estimated spawning date to estimate the time period that the larvae of each collection group were feeding until they were collected (Table 2). "Collection-group period" is defined as the time period from the time of first spawning to the time when larvae were sampled.

Estimated area occupied by larval cohorts

The yellowfin tuna larvae that were collected near the Frailes Islands may be recruited locally from offshore areas; this conjecture is based on measurements of the mean monthly fields of velocity and direction of the North Equatorial Countercurrent (NECC) (up to 0.25 m/s) (Fiedler, 2002), southerly surface winds (up to 5 m/s) (Fiedler, 2002), and the location and proportion of reproductively active female yellowfin tuna (Schaefer, 1998) that are found during June–September in the Panama Bight area (Fig. 2). The earliest back-calculated spawning date for a larva within each collection group was used to estimate the maximum amount of time the larvae within that group were exposed to environmental and feeding conditions (Table 2). This amount of time and the maximum current speed and direction during this season were used to calculate maximum average distances traveled and the potential area occupied by each collection group until sampled at the Frailes Islands (Table 2, Fig. 2).

Ichthyoplankton and oceanographic surveys

During 1990–92 ichthyoplankton and oceanographic sampling were conducted from a 25-ft Boston whaler along the Morro Puercos (P) and Punta Mala (M) transects (Fig. 1) (IATTC[1]; IATTC [2]; Lauth and Olson, 1996). Data collected from these surveys were used to describe the temporal variation of conditions within the planktonic community that may correspond to that of larval yellowfin tuna growth rates. In 1990, oblique bongo tows were made from the surface to 50 m along both transects with 335-μm mesh nets (Lauth and Olson, 1996). As a measure of relative abundance, standardized plankton volumes under 10 m^2 of sea surface were calculated by following procedures of Smith and Richardson (1977), and the estimates for each side of the

bongo were averaged. Beginning in 1991, a 0.6-m^2 Tucker trawl equipped with a 335-mm mesh net, flow meter, and temperature-depth logger was used to sample ichthyoplankton at discrete depths at only the Punta Mala shelf break (MSB). These surveys were designed to study the vertical distribution and *in situ* growth and starvation rates of tuna larvae and the abundance of their zooplankton prey (IATTC[1]; IATTC[2]). Two replicate tows of 4 to 5 minutes were made at each of three or four depth strata: 0–5 (stratum 1), 5–20 (stratum 2), 20–40 (stratum 3), and 40–60 m (stratum 4). Plankton volumes were standardized (Smith and Richardson, 1977) at each depth stratum and were added together for each sampling day to compare the mean plankton volumes collected by the Tucker trawl with those collected by the bongo tows of the previous year. Mean plankton volumes were compared between collection group periods by using a one-way analysis of variance (ANOVA), the Student-Newman-Keuls multiple range comparison test (SNK test), and a *t*-test for unequal variance (α=0.05) when appropriate (Zar, 1984). In 1991, all four depth strata were sampled, but in 1992 only the first three strata were sampled. Additionally, a 73-μm mesh net with a mouth area of 0.014 m^2 was nested inside the Tucker trawl in 1992 to collect microzooplankton simultaneously with all other plankters. The displaced volume of the microzooplankton was included in the total standardized plankton volume for each sampling day. Water temperatures, surface wind speeds (m/s), and salinity values (psu) were measured (described in Lauth and Olson, 1996) during each sampling day.

Plankton displacement volumes for all years were also standardized as plankton volume per volume of water filtered (mL/m^3) to compare mean values between years and with literature values. The mean of each standardized volume for the 1990 oblique tows (0–50 m) and for discrete depths between 0 and 40 m of the 1991 and 1992 data were compared between collection group periods by using ANOVA, the SNK test, and a *t*-test for unequal variance (α=0.05) (Zar, 1984).

Sea-surface temperatures and wind stress climatology

The oceanographic surveys provided physical data within a limited portion of the area where *Thunnus* larvae potentially occurred since hatching. Therefore, area- and time-specific (monthly averages within 1- by 1.5-degree areas) SSTs to 5 m depth and wind stress climatology data (all data sets based on a hindcast ocean analysis system model described by Ji et al. [1995]) for the estimated area of each collection group period (Table 2, Fig. 2) were accessed from the internet (IRI[4]). Wind velocities in m/s were calculated from wind stress values based on a constant drag coefficient of 1.3×10^{-3} (Sverdrup et al., 1942; Large and Pond, 1981; Ji et al.,

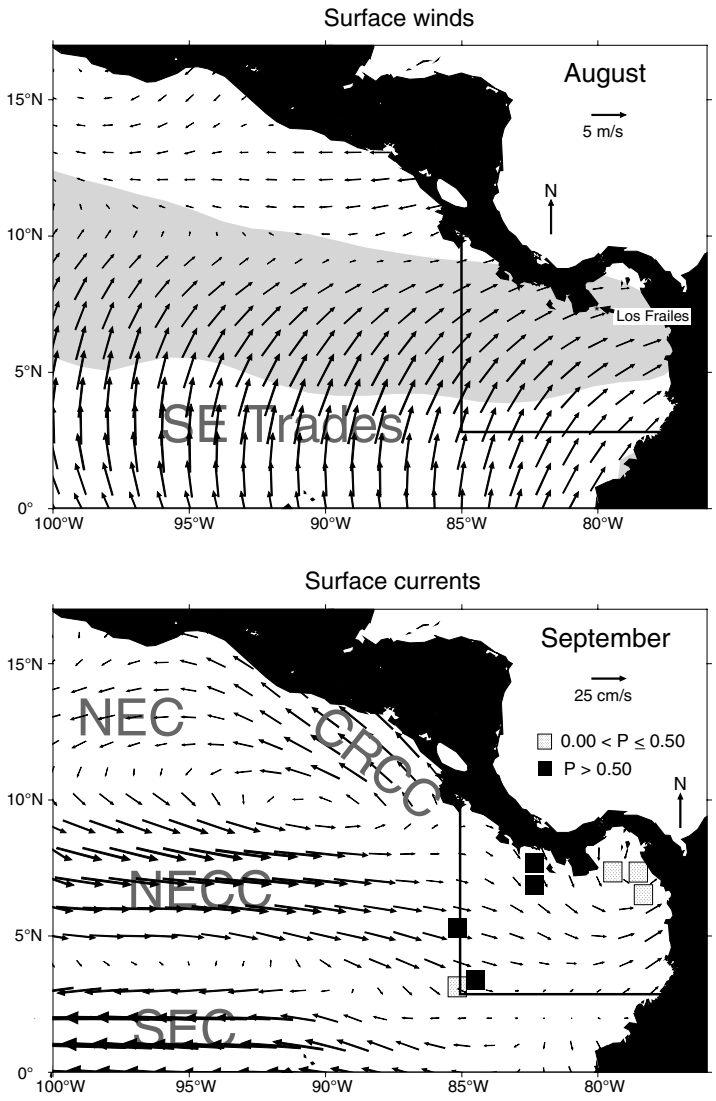

Figure 2

Monthly fields of surface wind velocity (for August) and surface current velocity (for September) representative of the seasonal extremes during the reduced upwelling period in the Panama Bight (after Figure 3 of Fiedler, 2002). Shading indicates surface wind divergence (intertropical convergence zone) during August, NEC = North Equatorial Current, SEC = South Equatorial Current, NECC = North Equatorial Counter Current, and CRCC = Costa Rica Coastal Current. The area between the vertical and horizontal lines and the land mass represents the estimated maximum average area (in degrees) (see Table 2) potentially occupied by each larval yellowfin tuna cohort during its life history. The spawning distribution of yellowfin tuna within the area is presented as the proportions (P) of reproductively active females in relation to the total numbers of mature females captured within 1-degree areas during the second and third quarters between 1987 and 1989 (from Schaefer, 1998).

[4] International Research Institute for Climate Prediction (IRI). 2006. Website: http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.Pacific/.monthly/ (accessed on 14 October 2005).

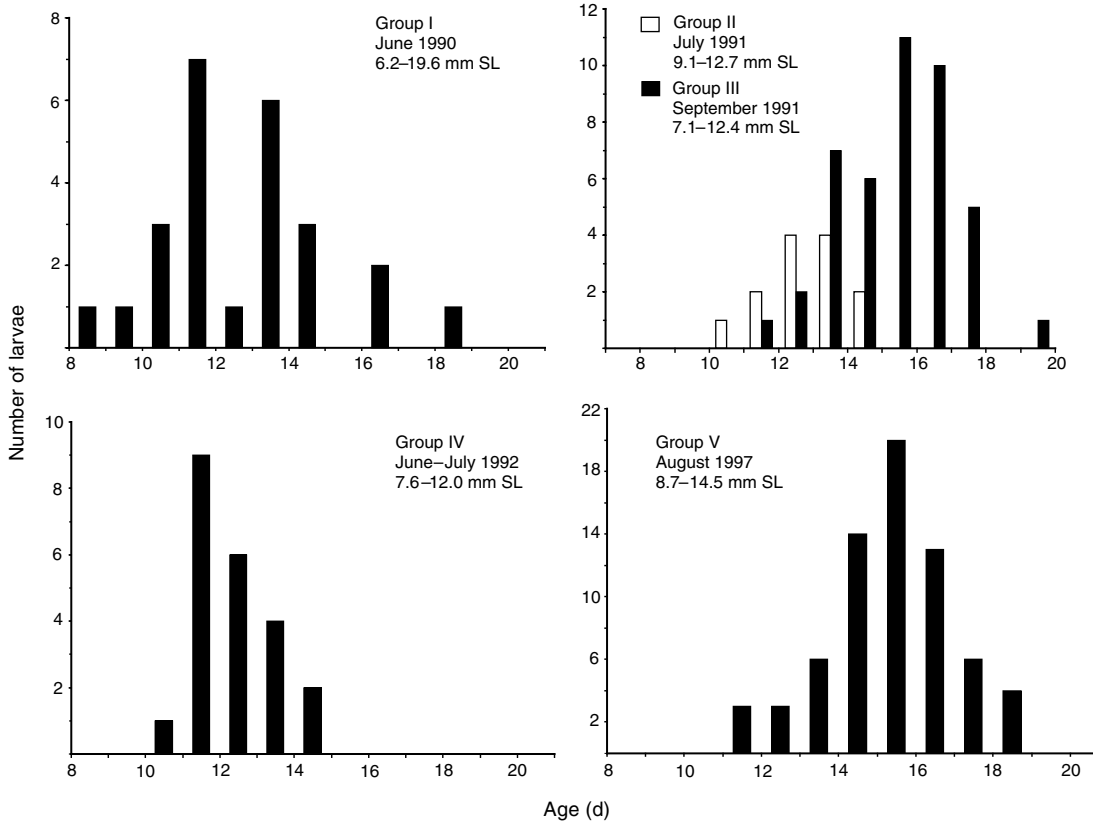

Figure 3

Age distributions and standard length ranges of yellowfin tuna (*Thunnus albacares*) larvae for each collection group period during 1990–92 and 1997. Larvae were collected near the Frailes Islands in the Panama Bight.

1995). Physical data were compared between collection group periods using ANOVA and the SNK test.

Results

Collections and identification

The occurrence of fairly large numbers (approximately 100 or more) of larval and early-stage juvenile *Thunnus* was sporadic, but not uncommon, in night-light collections during certain months of each year of the reduced upwelling season (Table 1). Based on back-calculated spawning dates and the average surface current speed, the collection site within an 8-degree latitude by 8-degree longitude area (between 2–10°N and 77–85°W) was estimated as the average maximum area potentially occupied by yellowfin tuna larvae of each collection group during their early life history (Table 2, Fig. 2). At the time of collection, sizes of larvae ranged from 6.2 to 19.6 mm SL (Table 1), and all were either in the flexion, postflexion, or transformation stages of development (stages described in Ambrose, 1996). Other scombrid species (i.e., *Auxis* sp., *Euthynnus lineatus*, and *Scomberomorous sierra*) were also found when *Thunnus* larvae were collected, but were not usually predominant in the collections.

Successful PCR amplification occurred in 80% of the larvae analyzed, and subsequent RFLP analysis indicated that the *Thunnus* larvae collected near the Frailes Islands were *T. albacares* (Table 1).

Size-at-age and growth

The ages of yellowfin tuna larvae collected ranged from 8 to 20 days (Table 1, Fig. 3). The age range was mostly limited between 11 and 14 days for the larvae collected in July 1991 (collection group II) and in June–July 1992 (collection group IV); therefore growth models were not fitted to the data (Figs. 3 and 4). However, a comparison of the size-at-age between all five groups within this limited age range indicated that both SLs and otoliths were significantly smaller for larvae collected in September 1991 (collection group III) (ANCOVA and Tukey multiple comparison test, $P<0.0001$), and that SLs were similar between the larvae of 1990 (collection group I) and July

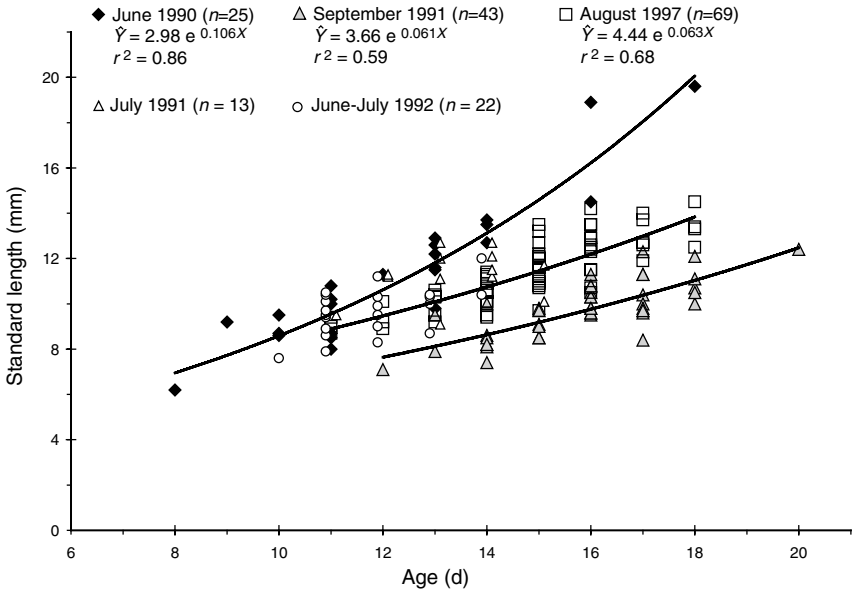

Figure 4

Exponential relationships between standard length and age in days estimated from otolith increment counts of larval yellowfin tuna (*Thunnus albacares*) collected during June 1990, September 1991, and August 1997. Data are also presented for yellowfin tuna larvae collected during July 1991 and June–July 1992, but growth models were not fitted to the limited range of data.

1991 (collection group II) and between those of 1992 and 1997 (collection groups IV and V).

The length-at-age data were used to examine and compare growth relationships of all yellowfin tuna larvae collected in June 1990, September 1991, and August 1997 (collection groups I, III, and V, respectively). An exponential model provided the best fit to each of the three groups of data (Fig. 4). The variances were homogeneous after log transformation of the length data for each group, and the slopes were compared. The slope and the average growth rate obtained through differentiation of the exponential equation of the 1990 data (1.28 mm/d, SE=0.134) were significantly greater than those of the September 1991 (0.60 mm/d, SE=0.033) and 1997 (0.71 mm/d, SE=0.038) data (ANCOVA, $P<0.0001$, Tukey multiple comparison test). The elevations (i.e., adjusted means or intercepts) of the 1991 and 1997 data were significantly different ($P<0.0001$) and indicated that the mean length-at-age was significantly smaller for larvae of the September 1991 collection group (Fig. 4).

Similar results were obtained for otolith growth rates (based on the exponential relationships between otolith diameter and age) for the three years (Fig. 5). The slopes were compared after log transformation of the otolith data for each group. The growth rate of the 1990 data was significantly faster than that of the 1991 and 1997 data (ANCOVA, $P<0.0001$, Tukey multiple comparison test), and the elevations were different between the 1991 and 1997 data, indicating that otoliths were significantly smaller for larvae of the September 1991 collection group (Fig. 5).

A comparison of the linear relationships between otolith diameter and SL (ANCOVA, $P<0.0001$, Tukey multiple comparison test; Fig. 6) revealed that the otoliths of the 1997 group were larger and grew significantly faster in relation to fish size than those of the 1990 and 1991 groups. Otoliths of the fastest (1990 group) and slowest (1991 group) growth periods were growing at the same rate in relation to fish length, but the slower-growing group had significantly larger otoliths in relation to fish size than those of the faster-growing group ($P<0.0001$; Fig. 6).

Standing stocks of ichthyoplankton

Ichthyoplankton and physical parameters were measured at four stations along the P and M transects on two sampling days in June 1990 (16 tows total, each to 50 m), at the MSB station on the M transect on six sampling days in June and July 1991 (12 tows each depth strata 1–4), at the MSB station on three sampling days in August 1991 (six tows each strata 1–4 and four tows each strata 1–3), and at the MSB station on two sampling days in June and July 1992 (six tows each strata 1–3) (Table 3, Fig. 1). The sampling days lay within the

period of time when each collection group of larvae could have been feeding in the estimated area of occurrence (Table 2, Fig. 2). Ichthyoplankton tows were not made in the Panama Bight during 1997.

Mean standardized plankton volumes were variable and significantly different (ANOVA, $P<0.001$) among collection-group periods (Fig. 7). The mean plankton volume (±SE) in 1990 (157.3 ±13.53 mL) when the fastest larval growth rate occurred was greater and different from all other sampling or collection periods (SNK test), and ranged from 106.5 to 310.4 mL under 10 m^2 of sea surface (Table 3, Fig. 7). The mean plankton volumes during June–July 1991 (82.3 ±3.46 mL) and during August–September 1991 (62.8 ±5.86 mL), when the slowest growth rate occurred, were similar and less than those for all other periods (SNK test); volumes ranged from 43.7 to 102.4 mL under 10 m^2 of sea surface (Table 3, Fig. 7).

Mean plankton volumes, expressed as the amount filtered per volume of water sampled within the first three depth strata, were also significantly different (ANOVA, $P<0.001$) among collection group periods. Means were similar between the 1990 and 1992 groups and between the two 1991 groups (SNK test). Volumes ranged from 0.199 to 0.559 mL/m^3 during 1990 and 1992 and from 0.075 to 0.235 mL/m^3 during the two 1991 periods (Table 3).

Plankton volumes included relatively large numbers of fish larvae (predominantly preflexion stages) during the least (August–September 1991) and most (June 1990) rapid growth periods, and mean values were not significantly different (t-test for unequal variances, $P>0.20$). Numbers of larvae under 10 m^2 of sea surface ranged from 686.8 to 4786.1 and from 934.5 to 2685.6 in 1990 and 1991, respectively. Few scombrid larvae occurred in the ichthyoplankton samples for each of the two years, but were greatest during the 1991 period. The number of scombrid larvae under 10 m^2 ranged from 0 to 2.7 and from 0 to 12.7 in 1990 and 1991, respectively. *Thunnus* larvae (preflexion stage) were collected only in August 1991, and the numbers ranged from 0.5 to 5.5 larvae under 10 m^2 of sea surface.

Environmental effects

Mean SSTs were significantly different among all collection group periods (ANOVA, $P<0.0001$). SSTs were similar between the local sampling area (Fig. 1) and the estimated region of each collection group (Fig. 2) in that they were significantly lower for the August–September 1991 period (group III) and higher for the July–August 1997 period (group V) (ANOVA, $P<0.0001$, SNK test; Table 2, Fig. 7).

The mean wind stress was significantly lower for the 1997 collection-group period (group V) when compared with all other group periods (ANOVA, $P<0.0001$, SNK test; Fig.7). The monthly means within each 1- by 1.5-degree area were similar and ranged from 0.084 to 0.517 dynes/cm^2 for group-collection periods I–IV, and for the 1997 period (group V), they ranged from 0.027 to 0.462 dynes/cm^2. Wind velocities calculated from the wind stress values were low to moderate, ranging from 1.59 to 3.94 m/s (modes of 2.45 and 2.60 m/s) for groups I–IV and from 0.90 to 3.72 m/s (modes of 1.2 and 1.7 m/s) for group V.

Higher salinity values, ranging from 33 to 34 psu, occurred during July–August 1997 (group V) during an ENSO event, and during the 1990–92 collection-group periods (I–IV) values ranged from 29 to 32 psu, when both the fastest and slowest growth rates of yellowfin tuna larvae occurred.

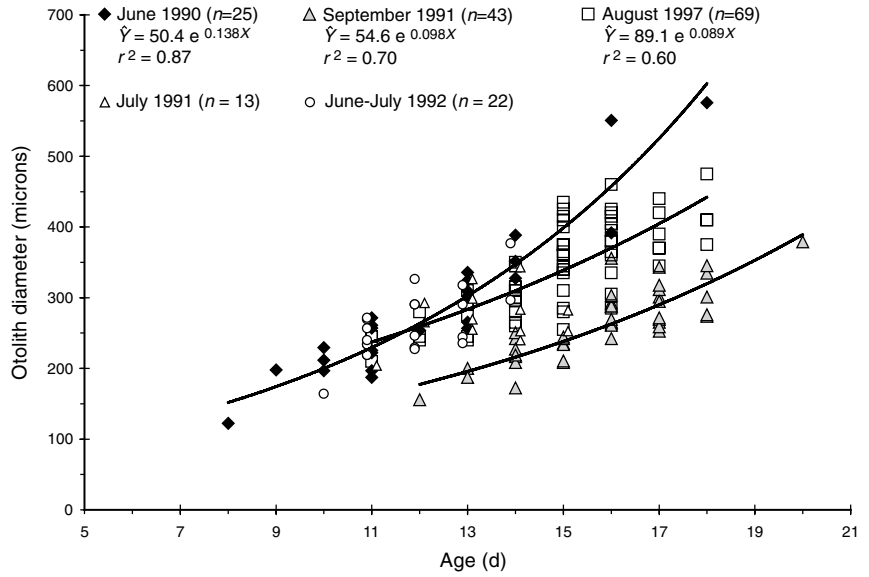

Figure 5

Exponential relationships between sagittal otolith diameter and estimated age in days of larval yellowfin tuna (*Thunnus albacares*) collected during June 1990, September 1991, and August 1997. Data are also presented for yellowfin tuna larvae collected during July 1991 and June–July 1992, but growth models were not fitted to the limited range of data.

Discussion

This study describes the first *in situ* growth rates for yellowfin tuna larvae occurring in the Pacific Ocean. Previous efforts to age and describe growth of yellowfin tuna during the early stages of develop-

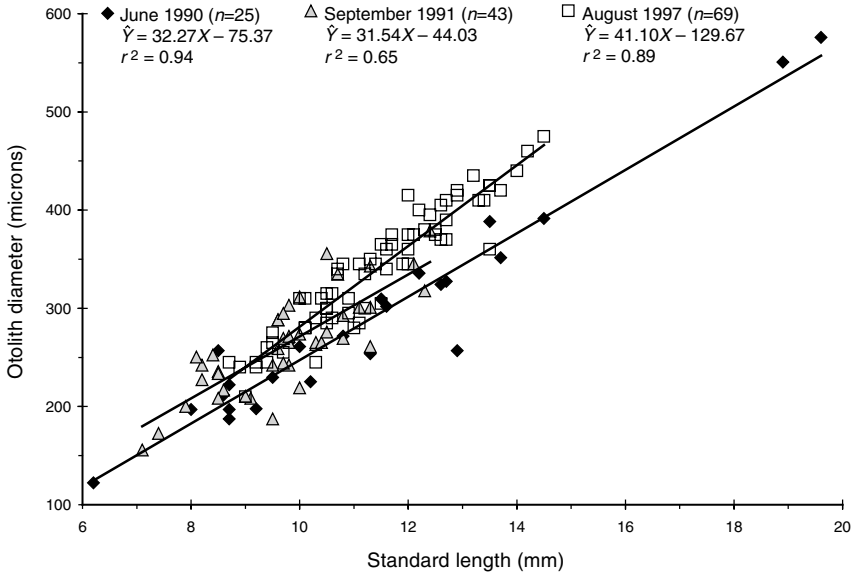

Figure 6

Linear relationships between otolith diameter and standard length for larval yellowfin tuna (*Thunnus albacares*) collected during June 1990, September 1991, and August 1997.

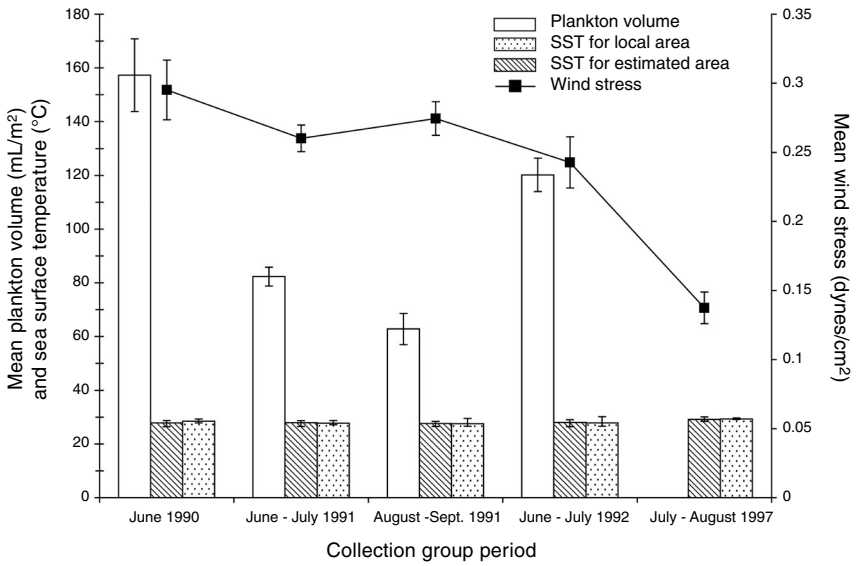

Figure 7

Standardized mean plankton volumes and monthly mean wind stress and sea surface temperature data for the local sampling area (Fig. 1) and the estimated area (Fig. 2) potentially occupied by each larval yellowfin tuna (*Thunnus albacares*) cohort during its life history. The standard errors of the means are indicated for plankton and wind stress, and the ranges for the mean water temperatures are also indicated. Plankton data were collected from ichthyoplankton tows in the vicinity of the Frailes Islands (see Fig. 1) and area- and time-specific physical data were extracted from the internet (IRI[4]).

Table 3

Standardized plankton displacement volumes collected from ichthyoplankton surveys conducted along the Punta Mala (M) and Morro Puercos (P) transects during 1990–1992 in the Panama Bight. Station definitions are described in Figure 1.

Sampling date	Transect	Station	Tow depth (m)	mL plankton volume/10m^2 of sea surface	mL/m^3	Sum of depth strata 1–4	Sum of depth strata 1–3
19 June 1990	M	MAB	0–50	121.3	0.219		
		MAB	0–50	242.3	0.425		
		MSL	0–50	123.9	0.226		
		MSL	0–50	118.5	0.208		
		MSB	0–50	143.0	0.260		
		MSB	0–50	156.0	0.280		
		MSH	0–50	167.6	0.328		
		MSH	0–50	310.4	0.559		
20 June 1990	P	PAB	0–50	140.9	0.252		
		PAB	0–50	129.1	0.264		
		PSL	0–50	205.8	0.393		
		PSL	0–50	163.6	0.301		
		PSB	0–50	113.2	0.199		
		PSB	0–50	125.6	0.240		
20 June 1990	P	PSH	0–40	106.5	0.245		
		PSH	0–40	149.5	0.333		
17 June 1991	M	MSB	0–5.7	6.6	0.117		
			5.3–25.8	21.5	0.105		
			21.2–27.0	39.6	0.147		
			43.1–48.1	2.4	0.049	70.1	67.7
		MSB	0–5.4	8.4	0.155		
			5.2–21.9	20.9	0.125		
			21.2–48.2	38.2	0.142		
			42.5–67.2	10.2	0.041	77.7	67.5
12 July 1991	M	MSB	0–5.7	13.0	0.229		
			5.4–21.9	31.5	0.190		
			22.9–44.5	23.9	0.111		
			43.8–67.2	10.5	0.045	96.9	68.4
		MSB	0–6.1	14.4	0.235		
			4.9–23.7	32.8	0.175		
			22.9–48.2	32.0	0.127		
			43.8–67.2	10.5	0.045	89.6	79.1
16 July 1991	M	MSB	0–5.7	9.9	0.176		
			4.9–21.9	19.9	0.117		
			21.2–44.5	24.7	0.106		
			40.2–67.2	12.4	0.046	67.0	54.5
		MSB	0–5.7	4.6	0.081		
			5.3–23.7	19.7	0.107		
			21.2–44.5	25.9	0.111		
			40.2–67.2	12.5	0.046	62.8	50.3
19 July 1991	M	MSB	0–5.4	6.2	0.114		
			5.2–21.9	24.4	0.146		
			20.2–44.5	36.4	0.150		
			40.2–64.0	15.5	0.065	82.5	67.0
		MSB	0–5.4	5.2	0.096		
			5.3–20.9	31.6	0.203		
			21.2–46.0	31.3	0.126		
			43.1–70.1	13.2	0.049	81.3	68.0

continued

Table 3 (continued)

Sampling date	Transect	Station	Tow depth (m)	mL plankton volume/10m^2 of sea surface	mL/m^3	Sum of depth strata 1–4	Sum of depth strata 1–3
23 July 1991	M	MSB	0–5.4	7.9	0.147		
			5.5–20.9	21.0	0.137		
			21.2–46.5	40.2	0.159		
			43.1–61.8	11.4	0.061	80.6	69.1
		MSB	0–5.7	9.7	0.171		
			5.5–22.9	18.5	0.116		
			21.2–46.5	40.8	0.162		
			41.8–67.2	15.0	0.059	83.9	68.9
25 July 1991	M	MSB	0–5.7	9.2	0.163		
			5.3–25.8	30.9	0.150		
			22.1–46.5	44.9	0.184		
			43.1–70.1	17.4	0.065	102.4	84.9
		MSB	0–5.4	9.4	0.174		
			5.1–20.9	23.3	0.147		
			21.2–38.9	34.5	0.195		
			43.1–62.3	25.9	0.135	93.2	67.2
15 August 1991	M	MSB	0–5.7	5.7	0.101		
			5.3–19.2	15.4	0.111		
			21.2–44.5	32.0	0.137		53.1
15 August 1991	M	MSB	0–6.7	8.6	0.129		
			5.3–21.9	24.3	0.146		
			21.2–44.5	29.5	0.126		
			36.0–56.5	15.6	0.076	78.0	62.4
		MSB	0–5.7	9.3	0.165		
			5.3–21.9	18.8	0.113		
			21.2–40.2	22.5	0.119		
			43.8–67.2	15.3	0.066	66.0	50.6
		MSB	0–5.7	8.6	0.151		
			5.7–21.9	20.2	0.125		
			22.9–43.8	27.7	0.133		56.5
		MSB	0–6.1	8.4	0.138		
			5.3–21.9	22.2	0.134		
			21.2–44.5	36.0	0.154		66.6
		MSB	0–5.7	12.3	0.217		
			6.1–19.2	18.5	0.142		
			21.2–48.2	53.6	0.199		84.3
21 August 1991	M	MSB	0–5.7	6.5	0.115		
			5.3–21.9	12.8	0.077		
			21.2–44.5	19.2	0.082		
			45.0–67.2	7.9	0.035	46.3	38.4
		MSB	0–6.4	5.4	0.084		
			5.5–21.9	12.3	0.075		
			21.2–44.5	18.5	0.079		
			43.8–67.2	7.5	0.032	43.7	36.2
23 August 1991	M	MSB	0–5.7	8.1	0.143		
			5.3–21.9	19.7	0.119		
			21.2–44.5	32.6	0.140		

continued

Table 3 (continued)

Sampling date	Transect	Station	Tow depth (m)	mL plankton volume/10m^2 of sea surface	mL/m^3	Sum of depth strata 1–4	Sum of depth strata 1–3
23 August 1991 (continued)			45.9–67.2	9.5	0.044	69.9	60.4
		MSB	0–5.7	7.3	0.128		
			5.3–23.7	23.4	0.127		
			21.2–44.5	31.2	0.134		
			43.1–67.2	10.9	0.046	72.9	61.9
22 June 1992	M	MSB	0–5.0	14.6	0.294		
			5.4–20.2	34.6	0.234		
			20.2–40.0	60.0	0.303		109.2
		MSB	0–5.0	11.5	0.233		
			5.0–20.2	39.3	0.259		
			20.2–40.0	52.4	0.264		103.3
		MSB	0–5.0	16.9	0.342		
			5.0–20.2	56.3	0.370		
			20.2–40.0	70.9	0.358		144.1
		MSB	0–5.0	23.4	0.473		
			5.0–20.2	54.5	0.359		
			20.2–40.0	54.2	0.274		132.1
2 July 1992	M	MSB	0–5.0	19.7	0.397		
			4.5–20.2	48.9	0.312		
			20.2–40.0	49.8	0.252		118.4
		MSB	0–5.0	10.7	0.216		
			5.4–18.7	37.5	0.280		
			20.2–40.0	65.9	0.333		114.0

ment may have been precluded by the patchiness in their distribution and the difficulties in species identification. The only other growth study done on yellowfin tuna larvae was conducted in the Gulf of Mexico (Lang et al., 1994), but the species identifications were based on morphology and meristics, and the larvae were younger than those in our study. Results from our mtDNA analysis enabled us to examine species-specific growth rates of older larval stages of yellowfin tuna and associated factors affecting their growth and distribution.

Distribution

Yellowfin tuna larvae have consistently appeared in the night-light collections near the Frailes Islands during the reduced upwelling season, but not during the season when strong upwelling occurs and other species of scombrid larvae and plankton levels are more abundant (Smayda, 1966; Forsbergh, 1969; Lauth and Olson, 1996). The absence of yellowfin tuna larvae from our sampling area during the upwelling season may be associated with a cessation of spawning by yellowfin tuna during this period (Schaefer 1998, 2001; Margulies et al., in press) and with the temperature threshold of their larvae. Lower mean water temperatures typically occur during the upwelling season (Lauth and Olson, 1996) and have ranged from 17.3° to 25.8°C within the upper 50 m (Owen[3]). In the laboratory, survival of first-feeding yellowfin tuna larvae is poor at ambient water temperatures of <21°C and at dissolved oxygen levels <2.2 mg/L (<33.0 % of oxygen saturation) (Margulies et al.[5]). These temperature and dissolved oxygen requirements probably determine and limit the distribution of yellowfin tuna larvae within the mixed layer and determine whether or not they can survive during the upwelling season when water temperatures are lower. The distribution of yellowfin tuna larvae during the upwelling season may also be strongly influenced by the occurrence of strong westerly directed currents and northerly winds resulting in larval transport away from the coastal areas of the Panama Bight during this season.

The area of larval distribution since hatching may actually be smaller or larger than what we have estimated, depending on the amount of passive transport and

[5] Margulies, D., V. P. Scholey, J. B. Wexler, R. J. Olson, J. M. Suter, and S. Hunt. In press. A review of IATTC research on the early life history and reproductive biology of scombrids conducted at the Achotines Laboratory from 1985 to 2005. Inter-American Tropical Tuna Commission, Special Report 16. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

the swimming behavior of the larvae within the mixed layer. Passive transport would probably occur only during the egg, yolk-sac, and first-feeding stages (the first 8–10 days after fertilization) because yellowfin tuna larvae are competent swimmers and can hold their position against strong currents in the laboratory beginning at around 8–10 mm SL (D. Margulies, personal commun.). Although the maximum average area of larval yellowfin tuna distribution from the time of hatching is probably our best estimate, the physical and biological processes that occur in such a large area may not be representative of processes occurring on much smaller scales that may be more specific to conditions affecting larval transport, growth, and survival (Owen, 1989).

Prey abundance

Our ichthyoplankton data were collected within a 0.5-degree area that included the Frailes Islands where larvae were sampled and may provide an index of prey abundance (at least for the first one or two weeks of feeding until piscivory occurs). Although our data were spatially limited, the measured plankton volumes provide the only available estimates of zooplankton levels for the periods of interest.

The use of different gear types (i.e., the bongo and Tucker trawl) for ichthyoplankton collections during 1990–92 may have affected the amount of microzooplankton sampled during the different years. Microzooplankton abundance has not been compared between these two types of sampling nets. However, Shima and Bailey (1994) reported that the bongo and 1-m Tucker nets caught similar numbers and size distribution of larval walleye pollock (*Theragra chalcogramma*). The higher plankton volumes collected by the bongo in 1990 may be an underestimate of plankton abundance compared to the volumes of water being sampled by the Tucker trawl with a larger mouth opening (McGowan and Fraundorf, 1966). Given that plankton volumes were probably under-represented in the bongo tows, the difference in magnitude between the amounts of plankton sampled by each net type may actually be greater.

Another potential bias in comparing plankton volumes among the different years was that more areas (stations) were sampled with the bongo in 1990 than with the Tucker trawl in other years (MSB station only). However, the mean plankton volume would have been similar in 1990 if only the MSB station had been used in the analysis (Table 3).

Growth

Daily growth rates estimated from the exponential models for each of the three years (1990, 1991, and 1997) ranged from 0.46 to 2.06 mm/d and were generally greater than those reported for other congeners (Jenkins and Davis, 1990; Lang et al., 1994). However, the larvae represented in those studies were predominantly younger and in earlier stages of development (and thus would exhibit slower absolute growth) than the flexion and postflexion larvae and transitional juvenile stages of yellowfin tuna collected in our sampling area. The slower growth rates observed in southern bluefin tuna (*Thunnus maccoyii*) larvae were also associated with density-dependent and oligotrophic conditions in the East Indian Ocean (Rochford, 1962; Jenkins and Davis, 1990; Young and Davis, 1990). Our growth rates, however, were comparable to similar developmental stages of other scombrids that inhabit relatively similar, productive nearshore waters, such as king and Spanish mackerels (*Scomberomorus cavalla* and *S. maculates*, respectively; DeVries et al., 1990), black skipjack (*Euthynnus lineatus*; Wexler, 1993), and little tunny (*Euthynnus alletteratus*; Allman and Grimes, 1998).

Distinct differences in the average size-at-age and growth rates were very apparent between our 1990 and September 1991 collections of yellowfin tuna larvae. Size-dependent processes (i.e., predation and starvation; Pepin, 1988; Grimes and Isely, 1996) or density-dependent growth and survival (Jenkins et al., 1991) may affect the size-frequency distributions of surviving larvae. A simulation model (Pepin, 1988) demonstrated that with increased food abundance, the mean and variance in larval growth rates increases, but, as predator abundance increases, the variance in growth rates decreases for any given mean. Instantaneous growth rates for yellowfin tuna larvae of a similar age in 1990 were 2 to 3 times higher than those in 1991, and plankton volumes were 2 to 7 times higher than those in 1991. Increases in food availability, such as that during 1990, may also attract predators and result in greater rates of mortality of the slowest-growing individuals, so that they are not represented in the sampled population. Although the larvae in 1991 were growing more slowly than those in 1990, they probably do not represent the slowest-growing larvae of their cohort. Typically, postflexion larval and early-stage juvenile scombrids collected during the reduced upwelling season in our sampling area have exhibited more variable growth (Wexler, 1993), but have been predominantly healthy (Margulies, 1993). Therefore, slower or faster growing survivors at this stage may be independent of their nutritional condition, and larvae collected by the sampling method we used represent the survivors and most competent individuals of their cohort.

Growth may have been slower in 1991 because of higher larval densities, limited food availability, and available prey composition. A strong inverse relationship exists between growth rates and stocking densities of yellowfin tuna larvae and early-stage juveniles (up to 18 days after hatching) fed a constant food supply in the laboratory (IATTC[6], IATTC[7]; Margulies et al.[5]). The re-

[6] IATTC (Inter-American Tropical Tuna Commission). 2000. Annual report of the Inter-American Tropical Tuna Commission 1998, 357 p. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

[7] IATTC (Inter-American Tropical Tuna Commission). 2002. Annual report of the Inter-American Tropical Tuna Commission 2001, 148 p. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

lationship may be even more pronounced under limited food conditions (Jenkins et al., 1991). Although we have only indirect evidence for density-dependent growth of the 1991 cohorts, the occurrence of more yellowfin tuna larvae sampled at the surface with the night light and the large numbers of other fish larvae collected in the ichthyoplankton tows coincident with the lower plankton volumes may indicate growth-limited conditions during this period. The slower growth of the late-stage larvae in 1991, when plankton abundance was much lower, may also be indicative of the types or species of preferred prey (zooplankters and fish larvae) that were available in the area that the larvae occupied. In the laboratory, yellowfin tuna larvae have predominantly selected all stages of cyclopoids over other types of copepods when offered a mixed assemblage of zooplankton prey (Margulies et al., 2001) and have become piscivorous beginning at approximately 6–7 mm in SL (Margulies et al.[5]). During this transitional stage in their diet, growth becomes much more rapid and variable (Kaji et al., 1999; Margulies et al.[5]), and the availability of specific types of fish larvae may influence their ability to switch to piscivory in the ocean. Yellowfin tuna larvae readily consume other, smaller conspecifics in the laboratory, but it is not known if there is a preference or growth advantage for consuming certain species of fish larvae during the transition to a more piscivorous diet. Although the available prey composition could affect the growth of late-stage yellowfin tuna larvae, intra- and interspecific competition for limited food resources during the 1991 period may have been the principal cause of slower growth.

The temporal variation in size-at-age within the same season and year (1991) may be related to the physical and biological characteristics of the area occupied by each group of larvae since hatching. Larval distribution could be determined by the location and timing of yellowfin tuna spawning and the small- and large-scale dynamics of physical oceanographic processes. Average sizes of the larvae and their otoliths of the 1991 August–September group were distinctly and significantly smaller than those of all other groups. The back-calculated first-feeding dates of this group coincided with the lowest plankton volumes measured in our local sampling area and with the only collection of first-feeding yellowfin tuna larvae from our ichthyoplankton tows. In contrast, the mean sizes of larvae and otoliths of the 1991 July group were similar to those of the fastest-growing group of 1990, despite low plankton volumes similar to those of the September 1991 period. We believe that the September 1991 group may have been spawned nearer to our local sampling area (Fig. 2) and that they were more exposed to feeding conditions in the vicinity of the Frailes Islands than were the faster-growing larvae of the July 1991 group.

Physical effects on growth

The probability of feeding success in marine larvae, and subsequent growth rates and survival, may increase with moderate levels of wind-induced microscale turbulence in their feeding environment (Rothschild and Osborn, 1988; Cury and Roy, 1989; Ware and Thomson, 1991; MacKenzie et al., 1994; IATTC[8], IATTC[9]). Preliminary estimates of wind speeds that produce optimal turbulent velocities and maximum survival of first-feeding yellowfin tuna larvae in the laboratory are moderate to high (D. Margulies, personal commun.) compared to wind speeds measured in the Panama Bight during this study. This estimate of optimal wind speeds is based on the assumption that maximum abundances of yellowfin tuna larvae in the EPO occur at depths of 0 to 20 m. However, the data on wind stress and velocities in the estimated area of larval distribution may not represent the frequency of optimal wind speeds associated with areas where first feeding of each cohort occurred. Additionally, wind event durations and frequencies, for which data were not available, may also play a significant role in the optimal survival of marine larvae (Wroblewski et al., 1989). Although moderate to high wind-induced turbulence may enhance early larval survival, growth rates may actually be slower during a portion of the larval phase as a result of higher larval densities and increased competition for limited resources.

Temperature-limited or -enhanced growth was not clear from our analyses of the yellowfin tuna larvae collected. Although a parabolic relationship between growth rates and SSTs was evident, it is unlikely that the two slowest-growing groups represented by the upper (29.1°C; group V) and lower (27.6°C; group III) mean temperatures in our study (Table 2) are approaching thermal tolerance limits for yellowfin tuna larvae. In the laboratory, successful hatching of yellowfin tuna larvae still occurs at upper temperatures of 32–34°C and first-feeding larvae are able to survive and feed between temperatures of 21° and 32°C (Margulies et al.[5]). Lower temperatures during the August–September 1991 (group III) period (Table 2) may have resulted in slower growth than that of the other collection periods, but we have only found significantly slower growth rates and differences in the mean sizes at first feeding when mean temperatures were less than 27°C in the laboratory (senior author, personal commun.). In contrast to the most rapid growth rate in 1990, the larvae in 1997 were growing more slowly when a strong ENSO event and the highest SSTs occurred. The optimum temperature range for growth of yellowfin tuna larvae in the Gulf of Mexico was 29–29.5°C (Lang et al., 1994), which was a similar temperature range for larvae of the 1997 period in our study. We do not, however, have information on relative food abundances during this

[8] IATTC (Inter-American Tropical Tuna Commission). 2001. Annual report of the Inter-American Tropical Tuna Commission 1999, 183 p. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

[9] IATTC (Inter-American Tropical Tuna Commission). 2002. Annual report of the Inter-American Tropical Tuna Commission 2000, 171 p. IATTC, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

time. Interactive effects of food availability and temperature may have a profound effect on growth, and we would expect that energetic demands become greater at the higher water temperatures, in which case the potential for faster growth would be attained through increased food consumption (Houde, 1989), providing food resources are not limited. Thus, it may be more reasonable to assume that food availability has a more significant impact on growth than SSTs during the reduced upwelling season when temperatures are consistently greater than 27°C.

Although water temperature has been shown to regulate the formation and short-term growth of otoliths in some marine fish species (Barber and Jenkins, 2001), the causal factor affecting otolith growth could also be associated with food availability (Govoni et al., 1985; Johnson et al., 2002) and composition (Woodbury, 1999). Otolith growth appears to be a conservative measure of somatic growth (i.e., otoliths continue to grow even with decreases in somatic growth; Campana and Neilson, 1985); therefore a significant change in otolith growth could signal a dramatic change in the larval feeding environment. We observed significant interannual differences between relationships of otolith size and fish size. Otoliths were disproportionately larger in slower growing groups of larvae, but additionally, during the period of 1997 when SSTs were abnormally high, otoliths were growing at a greater rate in relation to fish size (Fig. 6). Elevated water temperatures have been shown to increase short-term otolith growth (Hoff and Fuiman, 1993; Barber and Jenkins, 2001). Althoughtemperature may have affected otolith growth in 1997, lower food levels may have been the causal factor for a significantly slower otolith growth rate and the smaller mean otolith diameter of the 1991 group.

Recruitment implications

The probability of survival from early stages of development to recruitment in marine fishes is thought to be influenced by prerecruit starvation and predation mortality associated with slower growing and nutritionally weakened individuals (Cushing, 1975; Houde, 1987; Margulies, 2001) and predator-prey interactions and densities (Cowan and Houde, 1992). However, Peterman et al. (1988) have demonstrated that the survival rate of prerecruits older than 19 days of age is more variable than earlier life stages, and it is this stage that determines recruitment strength in northern anchovy (*Engraulis mordax*). Yellowfin tuna in the Pacific Ocean exhibit a pattern of reproduction that has strong potential for regulation of recruitment during prejuvenile stages, when initial numbers in a cohort are quite large and vital rates (e.g., growth, mortality) are high (Houde, 1987; Margulies, 2001). However, the potential for recruitment fluctuations is also high for the relatively long juvenile stage of yellowfin tuna as well (Houde, 1987; Margulies, 2001). In the EPO, yellowfin tuna are recruited to the fishery at a fork length of about 30 cm and at an age of approximately 6 months (Wild, 1994; Maunder and Harley[10]). Recruitment estimates calculated at quarterly intervals for yellowfin tuna in the EPO are variable and may be influenced by environmental fluctuations (Maunder and Harley[10]). It is not clear what effect slower or faster growing cohorts may have on recruitment, but the growth- and stage-specific mortality rates (Houde, 1987; Pepin, 1991; Comyns et al., 2003) of a cohort may determine whether it survives to recruitment or when it enters the fishery. We were unable to estimate mortality rates for the larvae collected in each of the three years because during some years they were collected on single sampling dates (Essig and Cole, 1986). Nonetheless, the recruitment estimate (ca. 1.44×10^7 individuals) following the period in 1991, when the smallest size-at-age and the slowest-growing larvae were present was approximately half the amount estimated (ca. 3.11×0^7 individuals) following the period in 1990 (Maunder and Harley[10]; Maunder[11]), when larvae were larger and growing more rapidly. The recruitment estimate following the 1997 period (ca. 3.06×10^7 individuals) was slightly less than that following the 1990 period. Larvae of the 1997 group were growing at a rate similar to that of the 1991 group, but the mean size-at-age was significantly greater, which may indicate a size advantage favorable for prerecruit survival (Miller et al., 1988). The growth rates and conditions estimated for yellowfin tuna larvae within the small scale area of our study may apply to localized recruitment estimates within the Panama Bight and not those of the entire EPO, given that restricted movements of yellowfin tuna occur in the EPO (Schaefer, 1991; Wild, 1994). Although these inferences may be applicable only to recruitment within the Panama Bight, they may still indicate that growth rates and the mean size-at-age during the larval and early-juvenile stages are a contributing factor to recruitment variability of yellowfin tuna in the EPO.

Our study provides the first examination of factors affecting larval growth and possibly prerecruit survival of yellowfin tuna in the Pacific Ocean. Future research is necessary to better understand small-scale variability in growth and mortality rates of yellowfin tuna larvae within their feeding environment. To that end, we are conducting further studies at the Achotines Laboratory in Panama to examine vital rates of this species and the interactions of these vital rates with biological and physical processes to complement our field measurements and to gain more insight into prerecruit survival of yellowfin tuna.

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