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REVIEW OF RESEARCH AT THE ACHOTINES LABORATORY

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1. INTRODUCTION

The egg, larval and juvenile stages of marine fishes are characterized by high rates of mortality and growth. Most marine fishes, and particularly pelagic species, inhabit complex ecosystems, and are highly fecund, producing very large quantities of small eggs and larvae. The identification of environmental or biological factors that are important in controlling survival during these early life stages is a potentially powerful tool in stock assessment.

Because vital rates (growth and mortality) during the early life stages of marine fishes are high and variable, small changes in those rates can have profound effects on the numbers of survivors and their potential for recruitment to fisheries (Houde 1989). Understanding and predicting the factors that influence pre-recruit survival are key goals of fisheries research programs.

2. RESEARCH ON THE EARLY LIFE HISTORY OF TUNAS

The Antigua Convention states that "the Commission shall perform the following functions, giving priority to tunas and tuna-like species:

(a) Promote, carry out and coordinate scientific research concerning the abundance, biology and biometry in the Convention Area of fish stocks covered by this Convention and, as necessary, of associated or dependent species, and the effects of natural factors and human activities on the populations of these stocks and species."

Although decades of research have provided considerable information on the populations of adult tunas, relatively little is known about the early life history stages and the factors that affect pre-recruit survival. Tunas are among the most commercially-valuable marine fish stocks in the world (FAO 2014), and recruitment variability is one of the most important factors affecting their abundance (IATTC 2004).

Tuna stocks are characterized by order-of-magnitude fluctuations in recruitment, but the underlying mechanisms controlling this variability remain poorly understood. Most tunas exhibit a pattern of high reproductive potential - spawning almost daily during their reproductively-active periods, and producing

millions of eggs per spawning (Schaefer 2001) - and pre-recruit life stages characterized by fast growth periods and high mortality (Davis *et al.* 1991, Tanaka *et al*. 1996, Margulies *et al*. 2007a). Yellowfin tuna (*Thunnus albacares*) are recruited to the surface fisheries in the eastern Pacific Ocean (EPO) at approximately 6 months of age (about 30 cm in length) (Aires-da-Silva and Maunder 2012). Recruitment in the EPO has fluctuated by a factor of 3.2 over the past 30 years (Minte-Vera *et al*. 2014). Like most tunas, yellowfin are highly fecund, and their early life stages are characterized by high mortality rates, high metabolic rates, and exponential growth (Margulies *et al.* 2007a, Wexler *et al*. 2007). This pattern of reproduction and growth and mortality during the larval or early-juvenile stages, when the numbers of fish are large and vital rates are high (Houde 1987, Margulies *et al*. 2001), is influenced by very small changes in the vital rates, and can potentially have a considerable effect on the subsequent recruitment of the survivors to the fisheries.

Prior to the 1980s, few studies had been undertaken to examine the mechanisms that control pre-recruit survival of tunas or to estimate their vital rates during their early life stages. These considerations motivated the IATTC to establish a research facility at Achotines Bay in the Republic of Panama for the purpose of studying the early life histories of tropical tunas and tuna-like fishes (scombrids).

3. THE ACHOTINES LABORATORY AND THE IATTC EARLY LIFE HISTORY PROGRAM

The Achotines Laboratory is located on the southern coast of the Azuero Peninsula in the Los Santos province of the Republic of Panama (Figure 1), in the northwestern portion of the Panama Bight. The continental shelf is quite narrow at this location; the 200-m depth contour occurs only 6 to 10 km from shore. This provides scientists working at the Achotines Laboratory with ready access to oceanic waters where spawning of tunas occurs during every month of the year. The annual range of sea-surface temperature in these waters is approximately 21° to 29°C.

The early life history research program involves laboratory and field studies of tropical scombrids, aimed at gaining insight into the recruitment process and the factors that affect it. Previous research on recruitment of non-scombrid fishes suggests that abiotic factors, such as temperature, light, current patterns, and wind conditions, and biological factors, such as feeding, growth, and predation, can affect recruitment (Houde 1997). As the survival of pre-recruit fishes is probably controlled by a combination of these factors, the IATTC research program addresses the interaction between the biological system and the physical environment (Lauth and Olson 1996, Owen 1997).

Research on tropical scombrids at the Laboratory has involved two distinct phases. The first phase, during 1984-1995, was directed predominantly at coastal, tropical scombrids, mainly black skipjack (*Euthynnus lineatus*), bullet and/or frigate tunas (*Auxis* spp.), sierra (*Scomberomorus sierra*), and striped bonito (*Sarda orientalis*). Since 1996, the focus shifted to the reproductive biology and early life history of yellowfin tuna, utilizing eggs spawned by broodstock yellowfin bred and held in captivity at the laboratory.

The Achotines Laboratory also periodically supports research by other IATTC scientists into bycatch reduction methods, as well as acoustic, behavioral, feeding, and tagging studies of tunas. In this report, we review the research conducted on the reproductive biology and early life history of yellowfin at the Achotines Laboratory. We also summarize the key research findings from these other studies, and present brief summaries of four areas of research that hold great promise for linkage with stock assessment research.

4. RESEARCH ON YELLOWFIN TUNA

4.1. Research on reproductive biology and early life history of yellowfin

Since 1996, the IATTC staff has conducted experimental research on the reproductive biology and early

life history in captivity of yellowfin (Margulies *et al*. 2016). The objective of the research is to develop a more complete understanding of daily processes occurring during pre-recruit (larval and early-juvenile) life stages, and how mortality is influenced by key environmental and biological factors. The ultimate goal of the program is to contribute new insights into recruitment variability. The ability to forecast yellowfin recruitment prior to the age at entry to the fishery (6 months), would be a powerful stock assessment tool.

Yellowfin research at the Laboratory has focused on important aspects of adult growth, spawning dynamics, genetics of spawning fish, early life stage development, growth dynamics of larvae and early-juveniles (in the laboratory and *in situ* (in the marine environment)), and the effects of physical factors on pre-recruit survival and growth. The results of this research are summarized in a series of publications listed on the IATTC website. Funding to support the research and infrastructure improvements required to conduct yellowfin research at the Laboratory has been provided by the IATTC, the Overseas Fishery Cooperation Foundation (OFCF) of Japan, the Japan International Cooperation Agency (JICA), and the Japan Science and Technology Agency (JST).

4.2. Key research findings from studies of yellowfin tuna

The studies of the reproductive biology and early life history of yellowfin tuna conducted since 1996 at the Laboratory have contributed significantly to our understanding of yellowfin biology and the factors that influence pre-recruit survival. The key findings of the program to date are as follows.

1. A standing spawning population of yellowfin was established in in-ground concrete tanks at the Laboratory. This was the first time that sustained spawning by yellowfin in land-based facilities had been achieved anywhere in the world, enabling the spawning dynamics, growth, genetics, physiology, and early life history of yellowfin to be studied over multiple years.

2. Methods for the successful capture, transfer, and husbandry of yellowfin were developed. A diet of 50% squid and 50% fish, typically thread herring or anchoveta, provides adequate nutrition for the yellowfin broodstock and fuels almost continuous spawning. Estimates of growth in length of captive fish, which ranged from 18 to 37 cm/year during 1996-2001 and 11 to 62 cm/year during 1999-2014, decrease with increasing length of the fish (Figure 2). Similarly, growth in weight, estimated at 11 to 26 kg/year and 4 to 36 kg/year during those same two periods, also decreased with increasing weight of the fish. The stable environment of the land-based tanks seems to promote good health and sustained spawning of yellowfin (Wexler *et al.* 2003).

3. The spawning patterns of yellowfin in relation to physical and biological factors have been described. The broodstock fish spawn as long as they receive adequate daily food rations and water temperature is above 23.3°C. Water temperature appears to be the main exogenous factor controlling the occurrence and timing of spawning (Figure 3). Courtship and spawning behaviors are ritualized, and yellowfin appear to adjust the timing and final maturation processes of spawning in response to minute changes in water temperature (Margulies *et al*. 2007b).

4. Female yellowfin in captivity start spawning at between 1.3 and 2.8 years of age, with an average of slightly less than 2.0 years. Over short periods (<1 month), spawning females increased their egg production by 30 to 234% in response to short-term increases of 9 to 33% in their daily food ration. The ability to increase egg production in response to increased availability of food has adaptive significance, and would allow yellowfin to exploit patchy food resources and periodic increases in productivity of prey in the ocean.

5. Genetic monitoring of the spawning yellowfin was conducted by comparing mitochondrial DNA variation in spawning females with that in their eggs and larvae. The analysis identified individual

spawning females and estimated their spawning periodicity. Female yellowfin are capable of spawning daily for extended periods of time, as long as they have sufficient food and the water temperature remains above 23.3°C.

6. There is a significant inverse correlation between water temperature and egg size, egg stage duration, larval size at hatching, and yolk-sac stage duration. Fertilized yellowfin eggs average 1.0 mm in diameter and 43 µg in dry weight. Hatched larvae average 2.5 mm in standard length (SL) and 30 µg in weight, while larvae at first feeding average 3.3 mm SL and 22 µg in weight. The growth potential from early-stage larva to size at recruitment (30 cm at 6 months of age) is very high, approaching 10^6 to 10^7 times.

7. Trials have been conducted at the Achotines Laboratory of the feasibility of bycatch-reduction devices, such as sorting grids and bubble curtains, which would allow smaller fish to escape from tuna purse-seine nets while retaining larger fish. Results indicated that yellowfin swim through sorting grids, but are reluctant to pass through bubble curtains. During 2016, two related research projects were supported by the Achotines Laboratory. In one project, a feasibility study funded by the European Union of the use of biodegradable and non-entangling materials to construct fish-aggregating devices (FADs), preliminary data were gathered on the durability of biodegradable materials for FAD construction. The other project, funded by the International Seafood Sustainability Foundation (ISSF), was a study by Drs. Gala Moreno and Guillermo Boyra of the acoustic properties of yellowfin as a means for discriminating among species in the purse-seine fishery. Analyses of the data are ongoing, and the preliminary results show promise for determining relationships between the strength of the acoustic signal and the size of the fish and the signal frequency for detecting yellowfin.

5. PROMISING LINKS BETWEEN YELLOWFIN EARLY LIFE RESEARCH AND STOCK ASSESSMENT

5.1. Laboratory and *in situ* growth of larval and juvenile yellowfin

Much of the experimental effort with yellowfin at the Achotines Laboratory has focused on growth dynamics during the pre-recruit stages. For larval and early-juvenile fish, it is not the mortality rate (*M*) alone that determines stage-specific survival, but also the ratio of mortality to growth (*M*/*G*), the stage-specific or 'physiological' mortality rate (*i.e.* mortality per unit of growth) (Houde 1997). Small variations in either the instantaneous mortality or specific growth rates can generate major changes in stock level at later stages. Growth variability alone has the potential to influence stage durations and cumulative mortality during the larval and juvenile life stages (Houde 1989).

Since 1997, studies have been conducted of growth of yellowfin larvae and juveniles reared from eggs from the yellowfin broodstock. Studies have focused on the effects of food availability, water temperature, and other physical factors on the survival and growth of larvae and juveniles up to 100 days after hatching. Early-larval growth (the first 2-14 days after hatching) is exponential in length and weight (<0.35 mm/day in length and 20-35% body weight/day), and accelerates significantly during the late-larval (15-24 days) and early-juvenile (25-100 days) stages (>0.6 mm/day and 30-50% body weight/day) (Figures 4 and 5). Yellowfin larvae become piscivorous at around 6.5 mm SL, and the timing of the onset of piscivory probably determines, in part, an individual's growth potential. Laboratory cohorts (groups of reared larvae from individual spawns) that are early piscivores (ca. 6.0-7.0 mm SL, which is early compared to most marine fish larvae) grow more rapidly, and individuals that remain zooplanktivorous lag in growth and/or are cannibalized. Early juvenile growth is rapid, ranging from 1.0 to 3.8 mm/day (Figure 6). In 2015, for the first time worldwide, early-juvenile yellowfin were transferred to, and reared in, a sea-cage anchored just offshore of the Achotines Laboratory. This now provides an opportunity to study experimentally, for the first time, the growth dynamics of a critical pre-recruit life

stage of yellowfin.

Growth rate variability in the larval and juvenile stages of marine fishes is substantial, and has strong potential to influence the *M*/*G* ratio during pre-recruit life stages (Houde 1997). Density-dependent regulation of growth has been identified as a significant potential factor in the control of pre-recruit survival (Shepherd and Cushing 1980, Rothschild 1986). For yellowfin, density-dependent mortality may weaken any relationship between egg production and recruitment, consistent with the IATTC stock assessment of yellowfin (Minte-Vera *et al*. 2014). It is possible that relative growth rate or density-dependence in feeding success and growth during the larval stage could contribute to variations in pre-recruit survival of yellowfin. Faster growth shortens the period of greatest vulnerability to mortality by predation. A larval or juvenile growth index for the Panama Bight, perhaps estimated quarterly, may prove useful as an index of recruitment strength (Margulies *et al*. 2007a). This type of sampling program to estimate *in situ* juvenile growth could be developed at the Achotines Laboratory via quarterly or seasonal sampling and aging of juveniles collected by nightlighting. We have conducted similar analyses of *in situ* growth during selected years in the Panama Bight, and we found some localized correspondence between high growth rates of larvae and recruitment estimates (Wexler *et al.* 2007). Our experimental results have indicated an early onset of substantial density-dependent growth of yellowfin during the first 2.5 weeks after hatching. Two- to fourfold increases in larval density have resulted in growth deficits of up to 56% during larval stages. We have also noted strong indirect evidence of density-dependent growth in larval cohorts during certain years in the Panama Bight (Wexler *et al.* 2007). Our experimental evidence suggests that density-dependence in growth of yellowfin persists into the early-juvenile stages. Even subtle density effects on growth during the relatively long pre-recruit juvenile stage (5 months) could have a "fine-tuning" effect on recruitment and the mean biomass of a cohort. This association will be studied experimentally at the Achotines Laboratory during 2017-2018.

5.2. Effects of wind-induced turbulence on survival of yellowfin larvae

The feeding success of marine fish larvae can be influenced by the levels of wind-induced microscale turbulence in the feeding environment (Rothschild and Osborn 1988, Cury and Roy 1989). For larvae, the probability of prey encounters and feeding success may increase with increases in wind-induced microscale turbulence up to an asymptotic level of wind and turbulence, and then decrease at higher levels of turbulence (MacKenzie *et al*. 1994). Our studies of feeding of yellowfin larvae in Japan in 1992 indicated a strong potential for the influence of microscale turbulence on the feeding success of yellowfin larvae. The investigations were expanded during 1997-2000 in a series of experiments at the Achotines Laboratory which examined the survival of larvae during the first week of feeding under variable conditions of microturbulence. Turbulence in the experimental tanks was measured as the mean horizontal velocity of a neutrally-buoyant surface drogue; in 1999 and 2000 these velocities were calibrated against velocities measured at depth with a microacoustic Doppler current meter. Preliminary results were reported by Kimura *et al.* (2004), and patterns of survival in response to experimental microturbulence were summarized in Margulies *et al.* (2016).

Our analysis of the 1997-2000 data indicates that survival during the first week of feeding is up to 2.7 times higher at intermediate levels of microturbulence (ca. $7.4 \times 10^{-9} m^2 s^{-3}$ to $2.25 \times 10^{-8} m^2 s^{-3}$ as an energy dissipation rate, a 3-dimensional level of current flow measured on a microscale) than at lower or higher levels of turbulence (Figure 7). A boundary layer model that equates microturbulence levels in the mixed layer of the ocean with wind speed produced estimates of optimal wind speeds for larval yellowfin survival of 2.0 to 4.5 m sec^{-1}, assuming maximum concentration of the larvae at depths of 5-20 m, estimated from larval field survey data in the literature. These are the first such estimates reported for early life stages of yellowfin, and among the first estimates of the effects of microturbulence on

survival of marine larvae based on extended experimental trials.

These estimates were examined for correlations with historical yellowfin recruitment in the EPO for 11 select 2°x2° areas. Wind speed data for the 1987-2007 period were obtained from the Blended Sea Winds Database, National Oceanic and Atmospheric Administration (NOAA), National Environmental Satellite, Data, and Information Service (NESDIS), National Climatic Data Center (NCDC) (Zhang *et al* 2006). The percentage of days with optimal wind speeds within a given 2°x2° area was estimated and correlations were calculated with IATTC quarterly estimates of yellowfin recruitment, with a 6-month time lag to account for pre-recruit development. A spatial pattern was observed both latitudinally and longitudinally (Figure 8). East of 100°W the areas closer to shore showed positive correlations, which became negative further offshore and west of 100°W. All five areas south of the equator exhibited positive correlations. The correlation analysis was also conducted for quarter-year combinations (*e.g*. quarters 1 and 2, quarters 1 and 3, *etc*.). For the six positively correlated areas in the southeast region of the study area (all the areas south of 5°N and east of 100°W), quarters 1 and 2 contributed most strongly to the positive correlation between optimal wind speed and recruitment. In all but one of these regions, the correlations became significantly positive when only the first two quarters of each year were considered (Area 11 off Peru was marginally non-significant). The four areas west of 100°W showed negative correlations regardless of quarter-year combination.

The wind speed-recruitment analysis, which is summarized in a recently completed draft manuscript, is promising for assessing yellowfin recruitment patterns, and can be refined and expanded. The correlation analysis involves variables with different spatial scales of (EPO-wide recruitment versus 2°x2° of wind speed). Wider geographical coverage would improve the analysis, and ongoing development of spatial components of the IATTC's recruitment estimates will allow wind speed data and recruitment to be examined on the same spatial scale.

5.3. Comparative studies of the early life histories of yellowfin and Pacific bluefin tunas

In 2011, the IATTC, Kindai University (KU) of Japan, and the Aquatic Resources Authority of Panama (ARAP) began a five-year comparative study of the reproductive biology and early life history of yellowfin and Pacific bluefin tunas, as part of the Science and Technology Research Partnership for Sustainable Development (SATREPS). The joint research project was funded through March 2016 by the Japan International Cooperation Agency (JICA) and the Japan Science and Technology Agency (JST), and has been conducted mostly at the Achotines Laboratory and the Fisheries Laboratories of Kindai University in Wakayama Prefecture, Japan. The experimental studies are the first in the world to investigate important comparative aspects of the reproductive biology, genetics, and early life histories of these two species of tuna. Although adult Pacific bluefin are temperate to subtropical, and adult yellowfin are tropical to subtropical, the early life stages of both species require warm-water (> 24°C) ecosystems as nursery grounds, thus providing a common background for comparative studies. Experimental results are being used to comparatively model mortality processes occurring during the pre-recruit life stages of both species. An additional objective of the project is to develop technologies for the aquaculture of juvenile yellowfin, including sea-cage culture. In 2015, for the first time worldwide, yellowfin early-juveniles were transferred to and reared in a sea cage located offshore from the Achotines Laboratory. Juveniles from this rearing series survived up to 158 days after hatch. Experimental research on juvenile yellowfin is being emphasized during 2017-2018.

Comparative experiments of larval stages of both species are ongoing during 2017, but preliminary results indicate that Pacific bluefin larvae hatch and initiate feeding at slightly larger sizes than yellowfin. Bluefin larvae, given their larger size and greater endogenous energy reserves, exhibit greater resistance to starvation at first-feeding compared to yellowfin, surviving 9 to 26 hours longer, depending on temperature. However, when small microzooplankton are the prevalent forage, the larger size of Pacific

bluefin larvae confers no apparent advantage in growth or survival (Figure 9); yellowfin larvae exhibit greater growth potential and higher survival when foraging on such. However, the greater size of Pacific bluefin larvae may confer feeding and growth advantages when foraging on large zooplankton, and this hypothesis is being experimentally investigated in 2017.

The results indicate that yellowfin and Pacific bluefin larval stages have different feeding patterns. Yellowfin use an opportunistic "bet-hedging" pattern of feeding, utilizing low or unpredictable levels of microzooplankton in their nursery habitats in the tropical and subtropical Pacific. Pacific bluefin show a "match-mismatch" pattern, surviving only if they find higher concentrations of prey, which may be created in their nursery areas of the western Pacific by eddies and convergent fronts. It is unclear, however, how predation pressure may interact with feeding success to influence the larval mortality dynamics of the two species.

5.4. The effects of ocean acidification on yellowfin eggs and larvae

Ocean acidification is a concern for its potential effects on the growth, development, and survival of early life stages of tunas in oceanic habitats and on the spatial extent of suitable nursery habitat for tunas. The 5th Intergovernmental Panel on Climate Change (IPCC) assessment (Stocker *et al*. 2013) estimates a global average decline in ocean surface pH of 0.30-0.32 by 2100 due to increasing concentrations of dissolved carbon dioxide (pCO_2) from anthropogenic activities. Across regions of the Pacific Ocean where yellowfin tuna spawn and develop, mean surface water pH is predicted to decrease by 0.26-0.49 pH units by 2100 (Ilyina *et al*. 2013).

To investigate the potential effects of ocean acidification on yellowfin early life stages, in 2011 a laboratory study was conducted by multiple collaborating organizations at the Achotines Laboratory to test the impact of increased pCO_2 on eggs, yolk-sac larvae, and first-feeding larvae. In two separate trials, acidification levels ranging from present day to those predicted to occur in some areas of the Pacific within the next 100 years (near future) to 300 years (long term) were tested. The results were variable between trials, but suggested significantly reduced size and survival of larvae (Figure 10), and prolonged egg hatch times at near-future acidification levels (Bromhead *et al*. 2015). Histological analysis of organ development in larvae indicated significant lethal and sub-lethal effects on larval organs at pH levels higher than those at which significant effects on survival and growth were detected (Frommel *et al*. 2016).

The potential impacts of ocean acidification on early life stages are an important consideration in future assessments of tunas in the EPO. A workshop was held in Sydney, Australia, in January 2016 to review the current status of information on the effects of ocean acidification on pelagic fisheries in the Pacific Ocean and to examine options for assessing the impact on tuna resources. The workshop report will be published in *Marine and Environmental Research*. If acidification does progress to predicted levels for the Pacific Ocean, it is unclear whether tunas will be able to adapt through selection for more resistant individuals (Bromhead *et al*., 2015). It is also unclear whether resistant traits are heritable (Munday *et al*., 2012). To date, there is evidence that near-future levels of ocean acidification can have significant negative effects on organ development, survival and growth of yellowfin eggs and larvae. These results allow models such as SEAPODYM (Lehodey *et al*. 2008) to be parameterised to include acidification effects, and to incorporate these effects in the development of spawning-habitat indices.

REFERENCES

Aires-da-Silva, A. and M. Maunder. 2012. Status of yellowfin tuna in the eastern Pacific Ocean in 2010 and outlook for the future. IATTC Stock Assessment Reports.

Bromhead, D., V. Scholey, S. Nicol, D. Margulies, J. Wexler, M. Stein, S. Hoyle, C. Lennert-Cody, J. Williamson, J. Havenhand, T. Ilyina, and P. Lehodey. 2015. The potential impact of ocean acidification upon eggs and larvae of yellowfin tuna (*Thunnus albacares*). Deep-Sea Res. II 113: 268-279.

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46: 670-680.

Davis, T.L.O., V. Lyne, and G.P. Jenkins. 1991. Advection, dispersion and mortality of a patch of southern bluefin tuna larvae *Thunnus maccoyii* in the East Indian Ocean. Mar. Ecol. Prog. Ser. 73: 33-45.

FAO. 2014. The state of world fisheries and aquaculture. FAO, Rome.

Frommel, A.Y., D. Margulies, J.B. Wexler, M.S. Stein, V.P. Scholey, J.E. Williamson, D. Bromhead, S. Nicol, and J. Havenhand. 2016. Ocean acidification has lethal and sub-lethal effects on larval development of yellowfin tuna, *Thunnus albacares*. J. Exp. Mar. Biol. Ecol. 482: 18-24.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symposium 2: 17-29.

Houde, E.D. 1989. Comparative growth, mortality and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87: 471-495.

Houde, E.D. 1997. Patterns and consequences of selective processes in teleost early life histories. *In* R.C. Chambers and E.A. Trippel (editors), Early Life History and Recruitment in Fish Populations, Chapman and Hall, London: 173-196.

IATTC-CIAT. 2004. Annual report of the Inter-Am. Trop. Tuna Comm. 2003, La Jolla, CA: 98 pp.

Ilyina, T., K.D. Six, J. Segschneider, R. Maier-Reimer, H. Li, and I. Nunez-Riboni. 2013. The global ocean biogeochemistry model HAMOCC: model architecture and performance as component of the MPI-Earth System Model in different CMIPS experimental realizations. J. Adv. Model. Earth Syst. 2013, http://dx.doi.org/10.1002/jame.20017.

Kimura, S., H. Nakata, D. Margulies, J.M. Suter, and S.L. Hunt. 2004. Effect of oceanic turbulence on the survival of yellowfin tuna larvae. Nippon Suisan Gabbaishi 70: 175-178 (In Japanese with English abstract).

Lauth, R.R. and R.J. Olson. 1996. Distribution and abundance of larval Scombridae in relation to the physical environment in the northwestern Panama Bight. Inter-Am. Trop. Tuna Comm., Bull. 21: 125-167.

Lehodey, P., I. Senina, and R. Murtugudde. 2008. A Spatial Ecosystem and Populations Dynamics Model (SEAPODYM) modeling of tuna and tuna-like populations. Prog. Oceanogr. 78: 304-318.

MacKenzie, B.R., T.J. Miller, S. Cyr, and W.C. Leggett. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnol. Oceanogr. 39: 1790-1799.

Margulies, D., J.B. Wexler, K.T. Bentler, J.M. Suter, S. Masuma, N. Tezuka, K. Teruya, M. Oka, M. Kanematsu, and H. Nikaido. 2001. Food selection of yellowfin tuna, *Thunnus albacares*, larvae reared in the laboratory. Inter-Am. Trop. Tuna Comm., Bull. 22: 9-51.

Margulies, D., V.P. Scholey, J.B. Wexler, R.J. Olson, J.M. Suter, and S.L. Hunt. 2007a. A review of IATTC research on the early life history and reproductive biology of scombrids conducted at the Achotines Laboratory from 1985 to 2005. IATTC Special Report 16.

Margulies, D., J.M. Suter, S.L. Hunt, R.J. Olson, V.P. Scholey, J.B. Wexler, and A. Nakazawa. 2007b. Spawning and early development of captive yellowfin tuna, *Thunnus albacares.* Fish. Bull. 105: 249-265.

Margulies, D., V.P. Scholey, J.B. Wexler, and M.S. Stein. 2016. Research on the reproductive biology and early life history of yellowfin tuna *Thunnus albacares* in Panama. Pages 77-114 *In*: D. Benetti, G.J.

Partridge, and A. Buentello (eds.), Advances in Tuna Aquaculture, Elsevier-Academic Press.

Munday, P.I., M.I. Mccormick, M. Meekan, K.L. Dixson, D.P. Chivers, and M.C.O. Ferrari. 2012. Selective mortality associated with variation in CO_2 tolerance in a marine fish. Ocean Acidif. 1: 1-6.

Owen, R.W. 1997. Oceanographic atlas of habitats of larval tunas in the Pacific Ocean off the Azuero Peninsula, Panama. Inter-Am. Trop. Tuna Comm., Data Report 9: 31 pp.

Rothschild, B.J. 1986. Dynamics of Marine Fish Populations. Harvard Univ. Press, Cambridge: 277 pp.

Rothschild, B.J. and T.R. Osborn. 1988. Small-scale turbulence and plankton contact rates. J. Plank. Res. 10: 465-474.

Schaefer, K.M. 2001. Reproductive biology of tunas. *In* B.A. Block and E.D. Stevens (editors), Fish Physiology, Vol. 19, Tuna: Physiology, Ecology, and Evolution, Academic Press, San Diego: 225-270.

Shepherd, J.G. and D.H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. J. Conseil. International pour Explor. de la Mer 185: 255-267.

Stocker, T.F., D. Qin, G.K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, B. Bex, and B.M. Midgley. 2013. IPCC, 2013: climate change 2013: the physical science basis. Contribution of Working Group 1 to the fifth assessment report of the Intergovernmental Panel on Climate Change.

Tanaka, M., T. Kaji, Y. Nakamura, and Y. Takahashi. 1996. Developmental strategy of scombrid larvae: high growth potential related to food habits and precocious digestive system development. *In* Y. Watanabe, Y. Yamashita, and Y. Oozeki (editors), Survival Strategies in Early Life Stages of Marine Resources, A.A. Balkema, Rotterdam: 125-139.

Wexler, J.B., V.P. Scholey, R.J. Olson, D. Margulies, A. Nakazawa, and J.M. Suter. 2003. Tank culture of yellowfin tuna, *Thunnus albacares*: developing a spawning population for research purposes. Aquaculture 220: 327-353.

Wexler, J.B., S. Chow, T. Wakabayashi, K. Nohara, and D. Margulies. 2007. Temporal variation in growth of yellowfin tuna (*Thunnus albacares*) larvae in the Panama Bight, 1990-97. Fish. Bull. 105: 1-18.

Zhang, H.-M., R.W. Reynolds, and J.J. Bates. 2006. Blended and gridded high resolution global sea surface wind speed and climatology from multiple satellites: 1987-present. Amer. Meteorological Soc., 2006 Annual Meeting, Paper #P2.23, Atlanta.

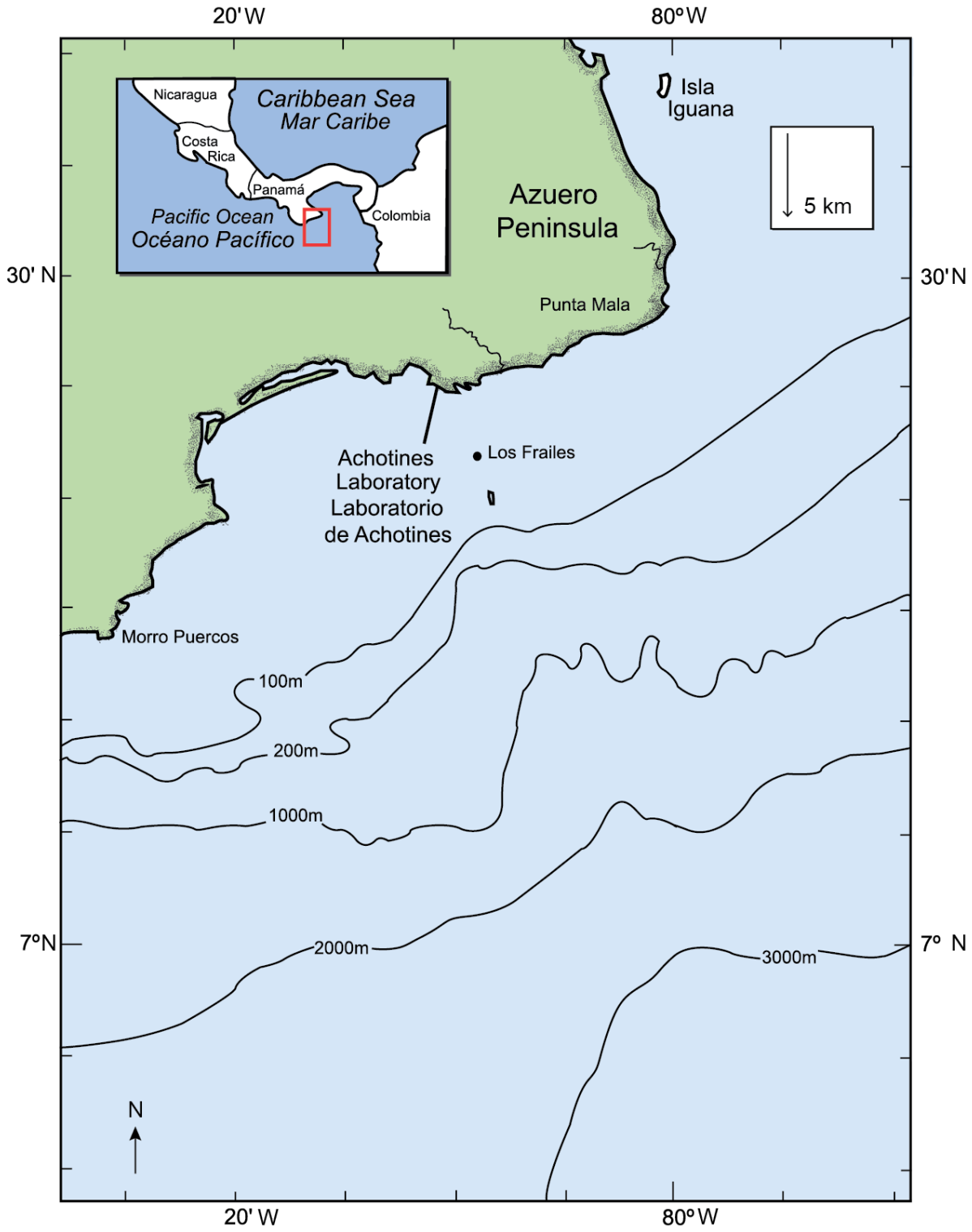


FIGURE 1. Location of the Achotines Laboratory, Republic of Panama.
FIGURA 1. Ubicación del Laboratorio de Achotines, República de Panamá.

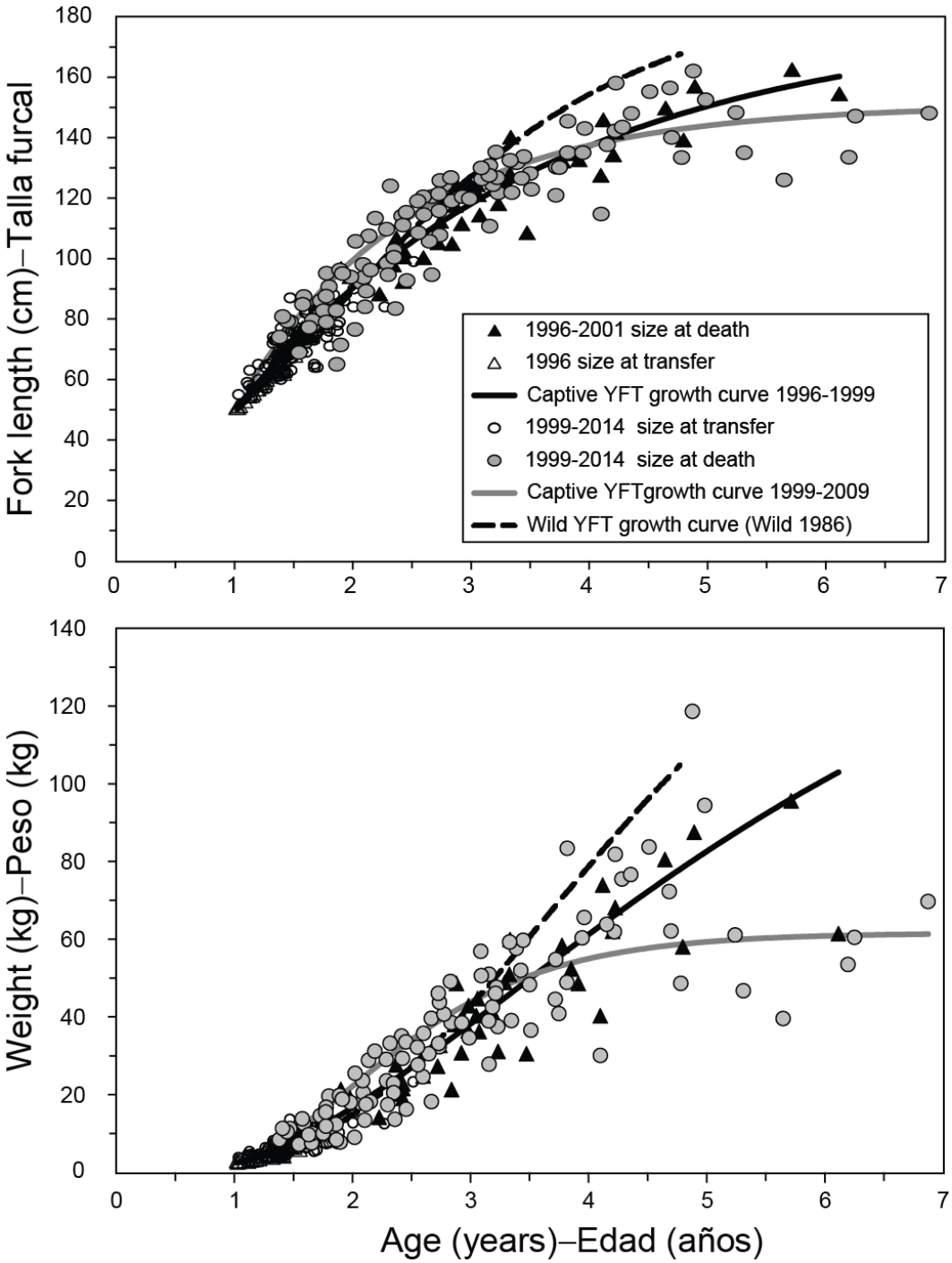


FIGURE 2. Relationships between length (top panel) and weight (bottom panel) and estimated ages of wild yellowfin in the eastern Pacific Ocean (Wild, 1986) and captive yellowfin in Tank 1. (After Wexler *et al*. 2003)

FIGURA 2. Relación entre talla (panel superior) y peso (panel inferior) y edad estimada de aletas amarillas en el Océano Pacífico oriental (Wild, 1986) y aletas amarillas cautivos en el Tanque 1. (De Wexler *et al*. 2003)

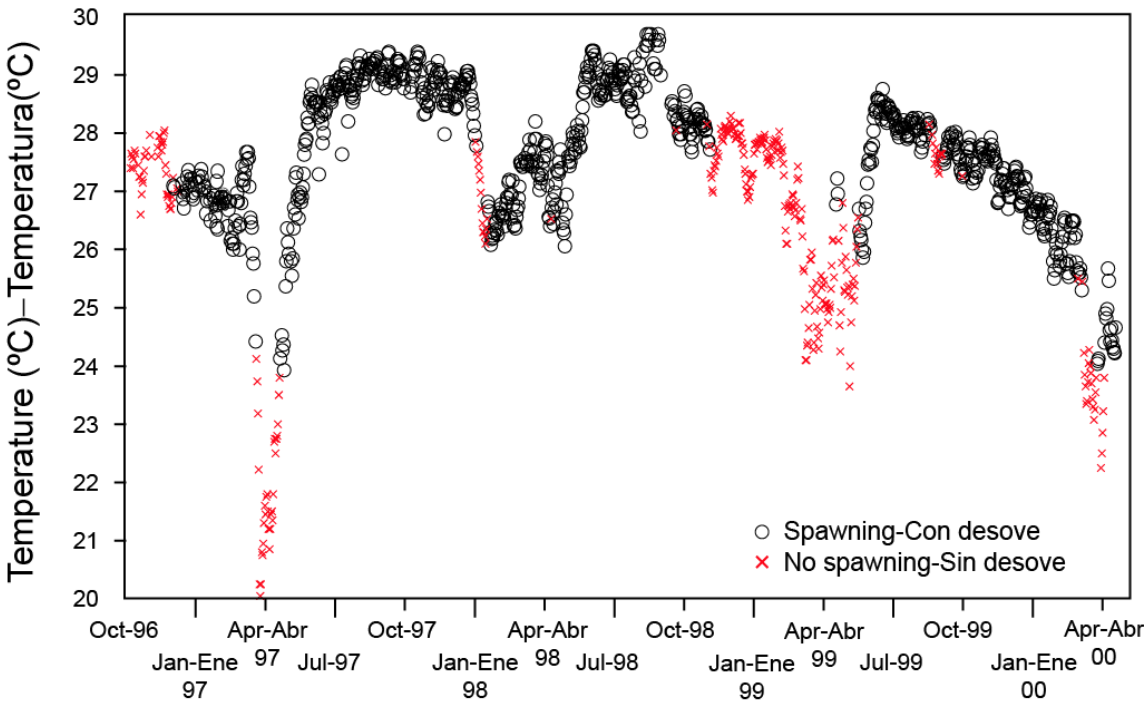
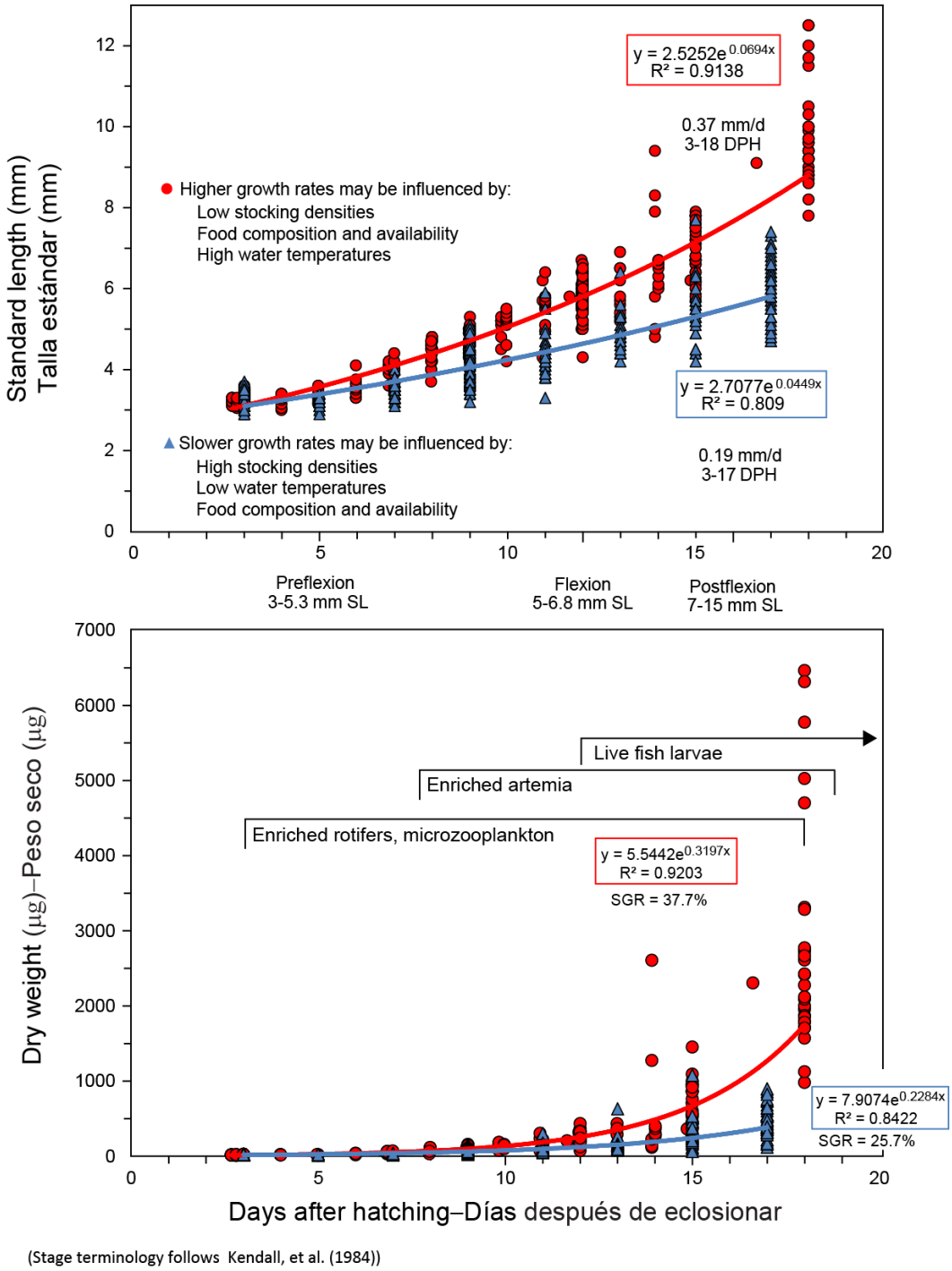


FIGURE 3. Mean daily water temperature in Tank 1. Plotted symbols are individual dates on which there was either spawning (indicated by 'o') or no spawning (indicated by 'x'). (After Margulies *et al*. 2007b)
FIGURA 3. Temperatura media diaria del agua en el Tanque 1. Los símbolos corresponden a fechas individuales en las que ocurrió desove (indicadas con 'o') a sin desove (indicadas con 'x'). (De Margulies *et al*. 2007b)



(Stage terminology follows Kendall, et al. (1984))

FIGURE 4. Relationships between standard length (top panel) and dry weight (bottom panel) and age in days after hatching of yellowfin reared in the laboratory for the fastest- (red line) and slowest-growing (blue line) cohorts. Prey type at age routinely offered in the laboratory and stage terminology at standard length are also shown.

FIGURA 4. Relaciones entre talla estándar (panel superior) y peso seco (panel inferior) y edad en días desde eclosión de aletas amarillas criados en el laboratorio correspondientes a las cohortes de crecimiento más rápido (línea roja) y más lento (línea azul). Se indican también el tipo de presa por edad ofrecido rutinariamente en el laboratorio y la terminología estándar de etapas por talla estándar.

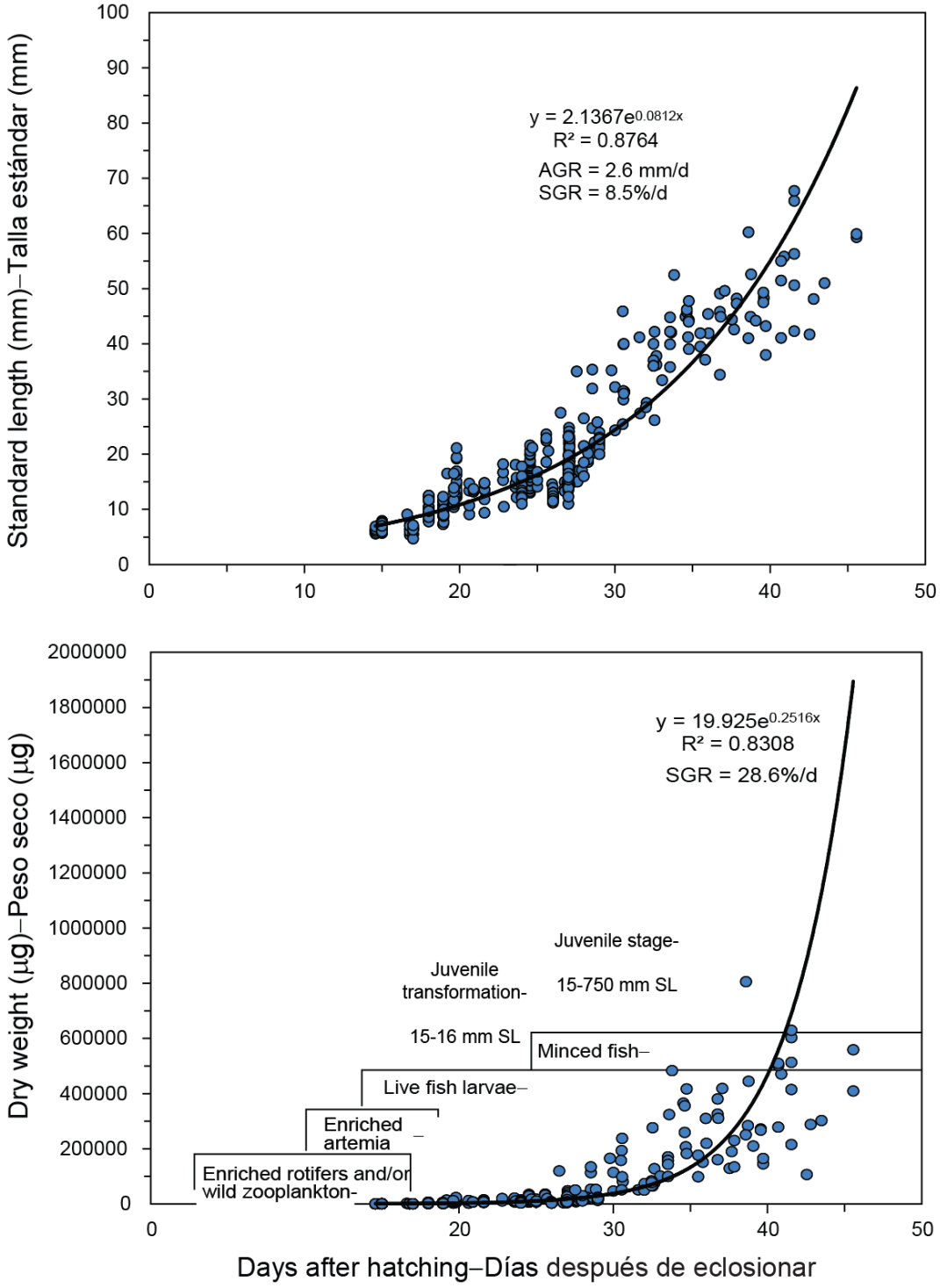


FIGURE 5. Growth in standard length (top panel) and dry weight (bottom panel) versus days after hatching of yellowfin larvae and early-juveniles reared in the laboratory. The bottom panel also shows the feeding regime.

FIGURA 5. Crecimiento en talla estándar (panel superior) y peso seco (panel inferior) como función de días desde eclosión de aletas amarillas larvales y juveniles tempranos criados en el laboratorio. En el panel inferior se indica también el régimen de alimentación.

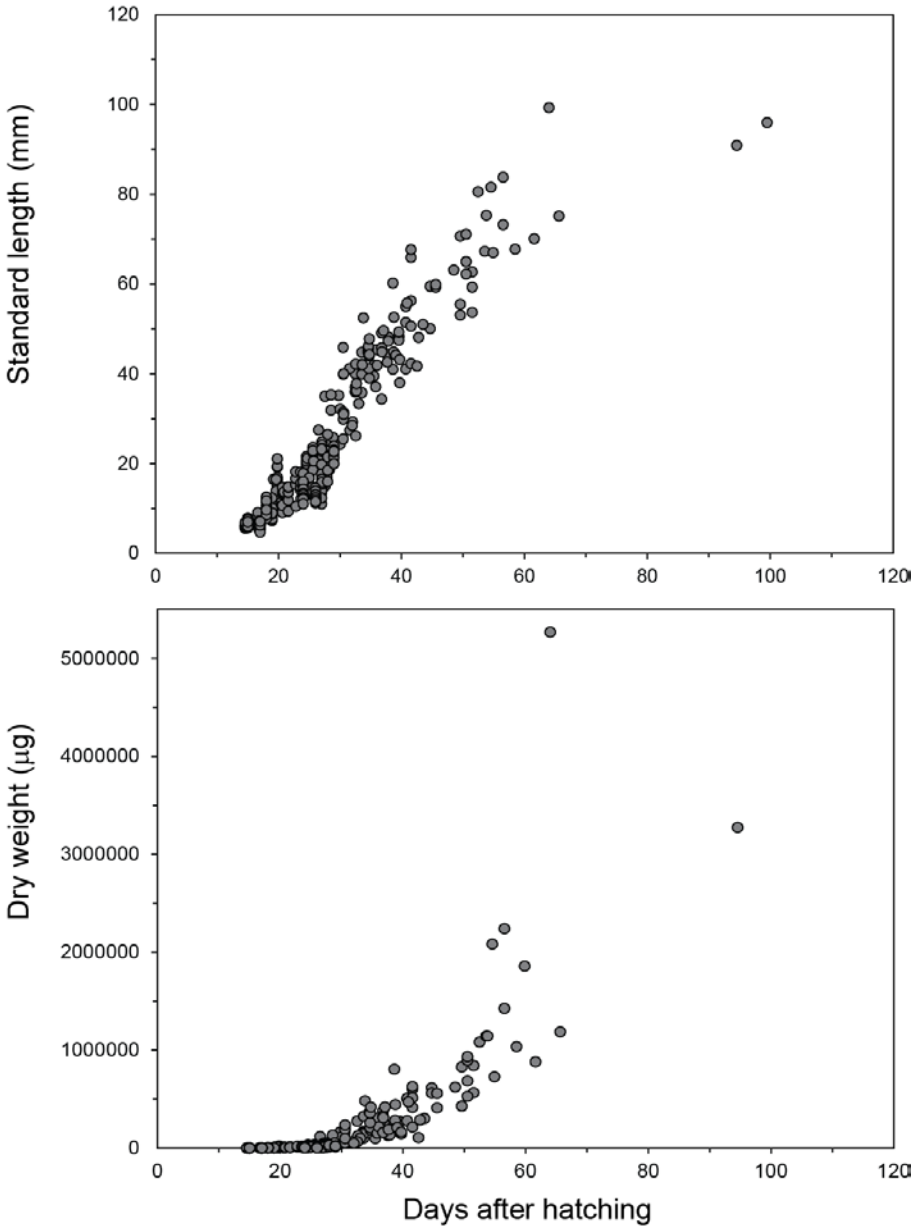


FIGURE 6. Growth in length (top panel) and dry weight (bottom panel) of yellowfin early-juveniles from 15 to 100 days after hatching in the laboratory.

FIGURA 6. Crecimiento en talla (recuadro superior) y peso seco (recuadro inferior) de aletas amarillas juveniles tempranos entre 15 y 100 días después de eclosionar en el laboratorio.

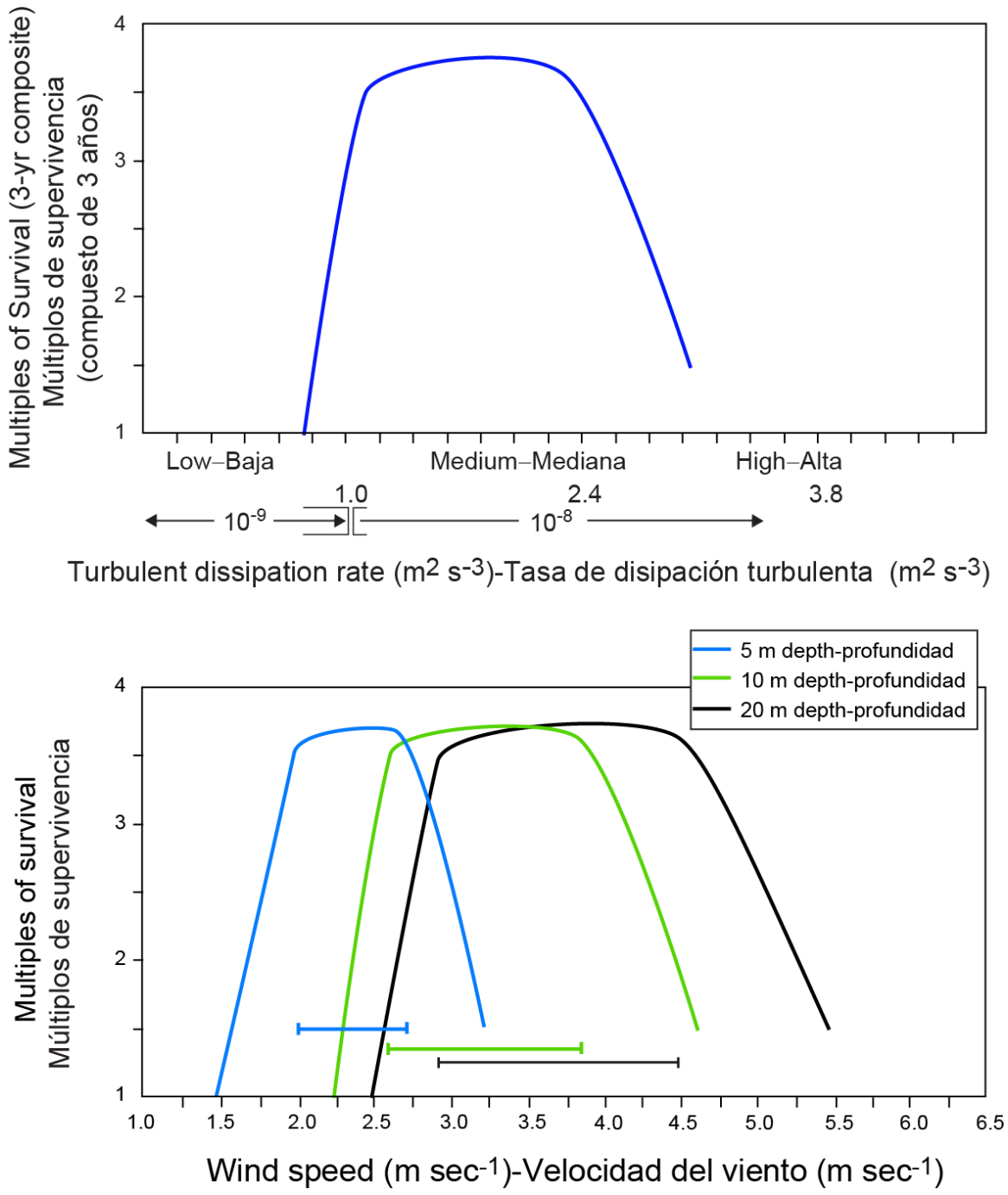
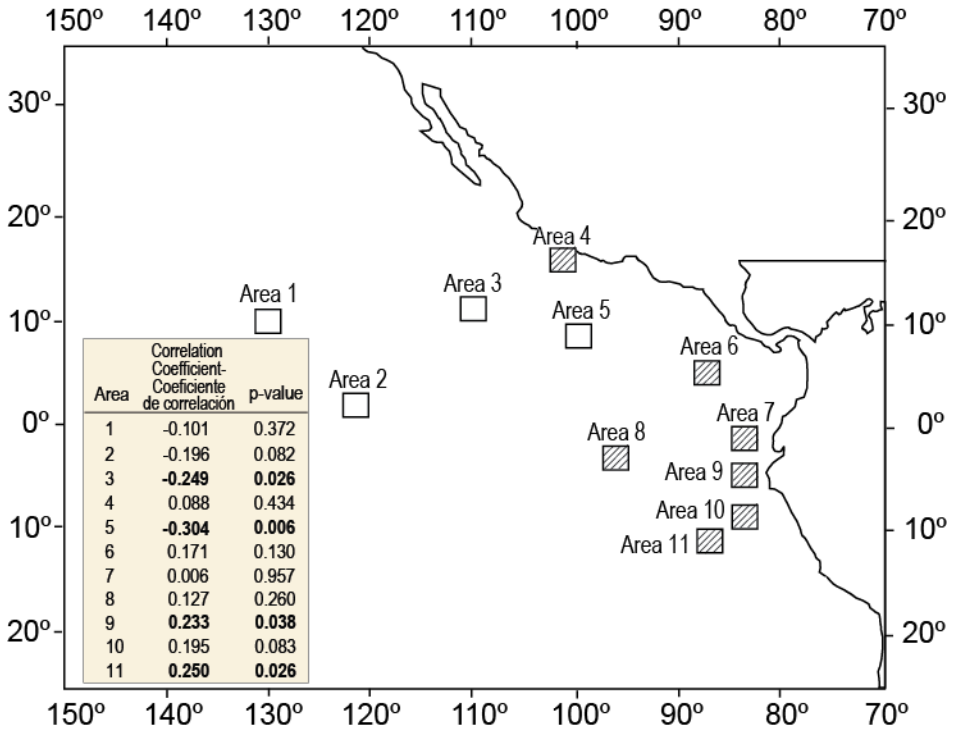


FIGURE 7. Relationship between microturbulence (estimated in the top panel as the turbulent dissipation rate and converted in the bottom panel to wind speed) and survival of yellowfin larvae during the first week of feeding. The survival curve is a smoothed, composite curve representing the mean survival estimated during 4 trials over 3 years.

FIGURA 7. Relación entre microturbulencia (estimada como tasa de disipación turbulenta y convertida en velocidad del viento en el panel inferior) y supervivencia de larvas de aleta amarilla durante la primera semana de alimentación. La curva de supervivencia es una curva compuesta suavizada que representa la supervivencia media estimada durante 4 pruebas en 3 años.



Area	Correlation Coefficient- Coeficiente de correlación	p-value
1	-0.101	0.372
2	-0.196	0.082
3	**-0.249**	**0.026**
4	0.088	0.434
5	**-0.304**	**0.006**
6	0.171	0.130
7	0.006	0.957
8	0.127	0.260
9	**0.233**	**0.038**
10	0.195	0.083
11	**0.250**	**0.026**

FIGURE 8. Correlation analysis results of recruitment (R) and the percentage of days with optimal wind speeds for selected 2°x2° areas of the eastern Pacific Ocean. Shaded boxes signify areas of positive correlation and open boxes negative correlation (bold values are statistically significant at an alpha level of 0.05).

FIGURA 8. Resultados del análisis de correlación del reclutamiento (R) y el porcentaje de días con vientos de velocidad óptima en áreas seleccionadas de 2°x2° en el Océano Pacífico oriental. Los cuadros sombreados señalan áreas de correlación positiva, y los blancos una correlación negativa (los valores en negritas son estadísticamente significativos en un nivel alfa de 0.05).

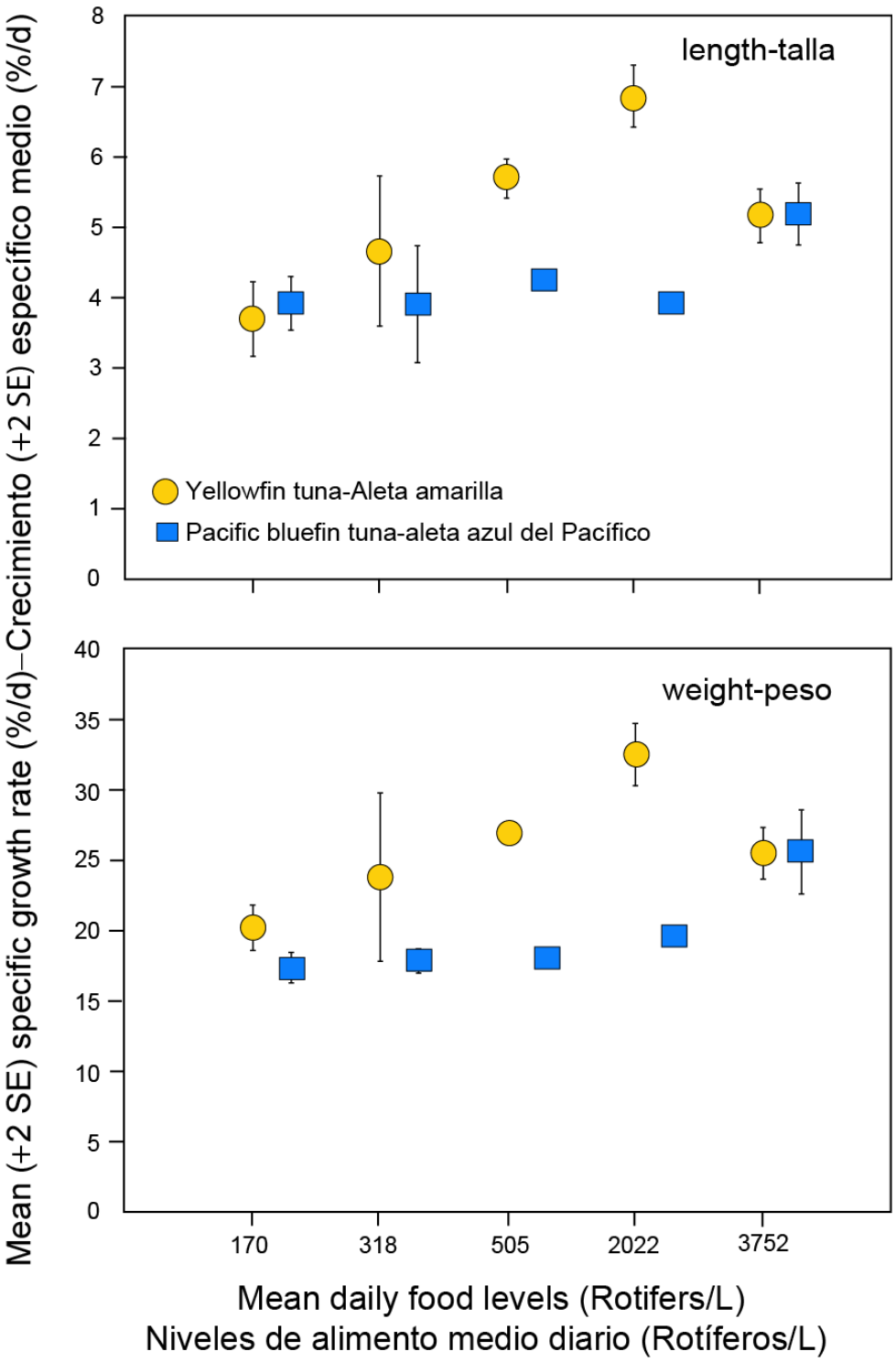


FIGURE 9. Mean specific growth rates in standard length (top panel) and dry weight (bottom panel) for yellowfin and Pacific bluefin larvae over a range of mean daily food levels during the first 10 days of feeding.

FIGURA 9. Tasas de crecimiento específico medio en talla estándar (panel superior) y peso seco (panel inferior) de larvas de aleta amarilla y aleta azul del Pacífico correspondientes a una gama de niveles de alimento medio diario durante los 10 primeros días de alimentación.

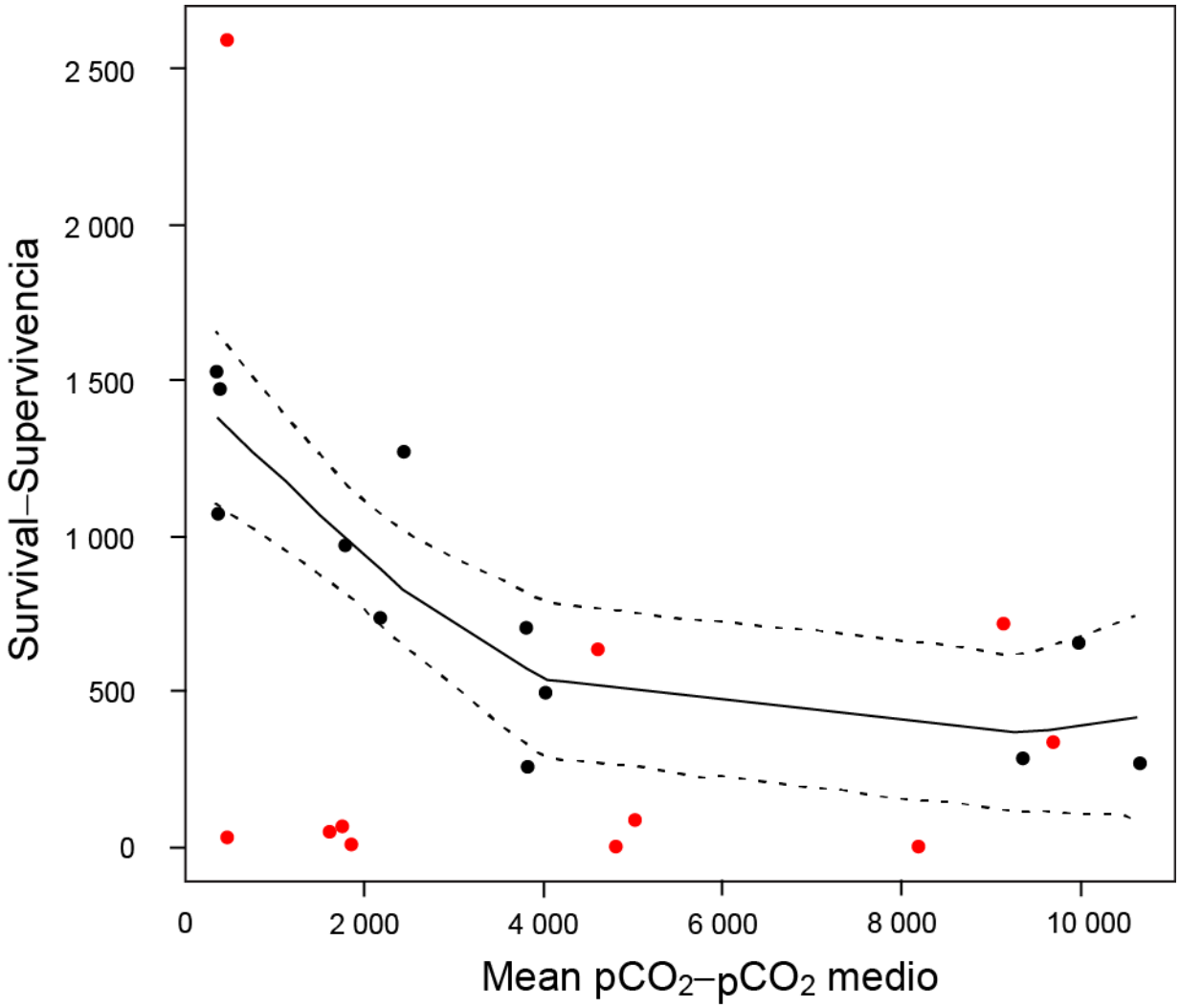


FIGURE 10. Predicted relationship between mean pCO_2 and yellowfin larval survival after 7 days of growth (Trial 1, black line) (Trial 2, red dots). Dashed lines for Trial 1 represent 95% confidence intervals; points indicate the data used to fit the models (Bromhead *et al.* 2015).

FIGURA 10. Relación entre pCO_2 medio y supervivencia de aletas amarillas larvales al cabo de 7 días de crecimiento (Prueba 1, línea negra) (Prueba 2, puntos rojos). Las líneas de trazos en la Prueba 1 representan los intervalos de confianza de 95%; los puntos indican los datos usados para ajustar los modelos (Bromhead *et al.* 2015).