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Ecology of larval fishes in the Independencia Bay, Pisco, Peru: Temporal and spatial relationships, taxonomic aspects

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...to my mother, Nancy

...to Evi + Eberhard Michler

...to the memory of my father (Hector A.), my brothers (Henry and Victor M.), my grandparents (Victor M. and Gilma R.) and my aunt (Nelly) who died during the time while I was working on my PhD.

That's exactly where betrayal of human values begins:
when the approach to science is merely scientific.

Romain Gary (1973)
In "The Gasp"

Contents

ABSTRACT

This study focuses on the identification, assemblage dynamics and distribution patterns of larval fish in the Independencia Bay, Pisco, Peru. The structure of the larval fish assemblages in the Bay was examined using a combination of univariate and multivariate techniques. The plankton of Independencia Bay was sampled monthly during the year 2000, to ascertain ichthyoplankton composition, abundance, and seasonality (Publication I); to determine diel abundance patterns and to assess the vertical variations of the dominant families in the area during a 24-hour cycle, and to relate observed variations to oceanographic parameters (Publication II). These data were used to assess the inferred function of the bay as a fish spawning and nursery ground.

The morphological development of some ichthyoplankton groups from the bay is described. In total, 16,156 fish larvae, representing 34 families, 48 genera and 48 species were collected. Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae and Atherinidae numerically dominated the diverse larval fish fauna and comprised 96.8% of the larvae captured; the remaining 3.2% included fish from several different families. The monthly mean density of total fish larvae showed two peaks. A springtime peak was dominated by newly hatched mote sculpins (Normanichthyidae) and newly hatched and pre-flexion anchovies (Engraulidae). A second, smaller, peak in summer was dominated by preflexion-stage anchovies, followed by mote sculpins. Greatest mean larval fish densities were recorded between September and November, suggesting a major spawning period. The greatest mean density during the spring peak was 7,492 larvae/100 m^3, recorded in October. The greatest mean density during summer was recorded in February (2,493 larvae/100 m^3). Concerning total larval abundance, there were no statistically significant differences between stations. Abundance in October (spring time) at Santa Rosa was higher than at the other three stations, but abundance in those other 3 stations was higher in February (summer time). The spring and summer ichthyoplankton abundance peaks in Independencia Bay coincided with high zooplankton standing stocks and also coincided, approximately, with periods of increased upwelling in the area. The occurrence of high larval fish densities and the wide range of larval stages suggest that Independencia Bay is a regionally important spawning and nursery ground for marine fish. A Principal Component Analysis (PCA) showed that temperature and salinity accounted for the largest fraction (74.4%) of the variability in the observed larval fish assemblage patterns. These conditions varied over time, station and water depth, however, interaction terms could not be clearly identified. Fitting a multinomial logistic model showed that larval fish assemblages and environmental conditions were associated in a complex way.

Vertical distribution patterns of ichthyoplankton were examined from two depths (surface and 10 m) at two stations (Panteón and Tunga). Blenniidae, Engraulidae, Gobiesocidae, Normanichthyidae, Atherinidae, and Labrisomidae numerically dominated the diverse larval fish fauna at Panteón, near La Vieja Island, and comprised 97.6% of the larvae captured. Gobiesocidae, Atherinidae, Pinguipedidae, Blenniidae, Engraulidae, and Labrisomidae were most abundant at Tunga, near the mainland coast, and comprised 77.6% of the larvae captured. The highest cumulative larval density and abundance in the water column was found at Panteón. The number of taxa (5) was the same at the surface at both stations, and was higher at 10 m depth at Tunga (26) than at Panteón (21). Two patterns of larval vertical distribution were observed. The larvae of most species were located mainly at 10 m, only the larvae of *Odontesthes regia regia* were found mainly at the surface. There were no statistically significant differences between nighttime and daytime densities of fish larvae at either depth. Nevertheless, a small degree of vertical redistribution was apparent for some species that could be interpreted as nocturnal dispersal.

The morphological development of two of the most abundant species from the bay is described in detail. Developmental series for individuals (recently hatched through transformation) of *Normanichthys crockeri* (Publication III) and *Prolatilus jugularis* (Publication IV) are presented using morphological features and pigmentation patterns. A total of 5,387 larvae (5,155 and 232 larvae of *N. crockeri* and *P. jugularis,* respectively) were identified. Ontogeny of both species is described and illustrated based on a total of 104 specimens (66 and 40 for *N. crockeri* and *P. jugularis,* respectively) ranging from 1.9 to 25.9 mm: recently hatched larvae through transformation stage. Larvae hatch size, information concerning the different stages (preflexion, flexion, postflexion and transforming), main diagnostic features of the larvae and meristic information including fin ray accounts are given. Osteological analysis of *N. crockeri* was also performed (Publication III). A total of 49 specimens were illustrated (see Publications III, IV and Appendix 6) to show pigmentation and morphological features of the larvae from Independencia Bay**.** These illustrations will be used for a guide to the ichthyoplankton of the bay (*in preparation*), and will be completed with ecological and meristic information.

ZUSAMMENFASSUNG

Die vorliegende Untersuchung hatte das Ziel, Fischlarven der Independencia-Bucht, Pisco, Peru zu identifizieren und deren Gemeinschaftsdynamik und Verteilungsmuster zu analysieren. Durchgeführt wurde diese Untersuchung anhand einer Kombination von univariaten und multivariaten Analysen. Das Plankton der Independencia-Bucht wurde im Jahr 2000 beprobt, um die Ichthyoplankton-Zusammensetzung, die Abundanzen und eine eventuelle Saisonalität festzustellen (Veröffentlichung I), die Tagesperiodik zu bestimmen, die Vertikalwanderungen der dominanten Familien in dem Gebiet während eines 24-Stundenzyklus auszuwerten und diese Veränderungen mit ozeanographischen Parametern in Beziehung zu setzen (Veröffentlichung II). Diese Daten wurden genutzt, um die Rolle der Bucht als Laich- und Aufzuchtgebiet zu erfassen. Zudem wurde die morphologische Entwicklung einiger Arten des Ichthyoplanktons dieser Bucht beschrieben. Insgesamt wurden 16.156 Fischlarven aus 34 Familien, 48 Gattungen und 48 Arten bestimmt. Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae und Atherinidae dominierten mengenmäßig die diverse larvale Fischfauna und stellten 96,8% der gefangenen Larven dar; die restlichen 3,2% entfielen auf verschieden andere Familien. Die monatliche Durchschnittsdichte aller Fischlarven zeigte zwei Maximalwerte: eine im Frühjahr, dominiert durch neu geschlüpfte *mote sculpins* (Normanichthyidae) sowie frisch geschlüpfte Anchovies (Engraulidae) im “preflexion-Stadium“. Die größte Durchschnittsdichte larvaler Fische wurde zwischen September und November vorgefunden, was auf eine Hauptlaichperiode im Frühjahr hindeutet. Die größte Durchschnittsdichte zu dieser Jahreszeit wurde im Oktober mit 7.492 Larven/100 m^3 ermittelt. Ein zweites kleineres Maximum wurde im Sommer beobachtet, das von Anchovies im preflexion-Stadium dominiert wurde, gefolgt von *mote sculpins*. Die größte Durchschnittsdichte in den Sommermonaten wurde im Februar gemessen (2.493 Larven/100 m^3). Hinsichtlich der Gesamtabundanz der Larven gab es keine statistisch signifikanten Unterschiede zwischen den Stationen. Bei Santa Rosa war die Abundanz im Oktober (Frühjahr) höher als an den anderen drei Stationen, aber bei diesen anderen drei Stationen war die Abundanz im Februar höher (Sommer). Die Frühljahrs- und Sommerabundanzen des Ichtyoplanktons der Independencia-Bucht zeigten ein Maximum, das mit hohem Zooplanktonvorkommen einherging. Zudem deckt sich das Maximum ungefähr mit Perioden stärkeren Auftriebs in dem Gebiet. Das Vorkommen saisonal hoher Fischlarvendichten und das weite Spektrum larvaler Stadien lässt vermuten, dass die Independencia-Bucht ein regional wichtiges Laich- und Aufwuchsgebiet für marine Fische ist. Die Principal component-Analyse der (PCA) zeigte, dass der größte Teil (74,4%) der beobachteten Variabilität der Gemeinschaftsstruktur auf die abiotischen Parameter Temperatur und Salinität zurückzuführen ist. Diese Bedingungen änderten sich über die Zeit,

die Stationen und die Wassertiefe. Interaktionen konnten nicht klar identifiziert werden. Die Anpassung eines multinominal-logistischen Modells zeigte jedoch, dass die Fischlarvengemeinschaften mit Umweltbedingungen komplex verknüpft waren. Vertikale Verteilungsmuster von Ichthyoplankton wurden an zwei Stationen (Panteón und Tunga) auf zwei Tiefen (Oberfläche und 10 m) untersucht. Blenniidae, Engraulidae, Gobiesocidae, Normanichthyidae, Atherinidae und Labrisomidae dominierten zahlenmäßig die larvale Fischfauna bei Panteón nahe der Insel La Vieja und machten 97,6% der gefangenen Larven aus. Gobiesocidae, Atherinidae, Pinguipedidae, Blenniidae, Engraulidae und Labrisomidae kamen am häufigsten bei Tunga vor, nahe der Festlandküste, und machten 77,6% der gefangenen Larven aus. Die höchste Larvendichte und das häufigste Vorkommen in der Wassersäule wurden bei Panteón gefunden. Die Anzahl der Taxa war an der Oberfläche beider Stationen identisch (5), jedoch auf 10 m Tiefe bei Tunga (26) höher als bei Panteón (21). Zwei vertikale Verteilungsmuster der Larven wurden beobachtet: Larven der häufigsten Arten wurden überwiegend um 10 m gefunden, wohingegen *Odontesthes regia regia* überwiegend an der Oberfläche gefangen wurde. Hinsichtlich der Fischlarvendichte gab es in beiden Tiefen keine statistisch signifikanten tageszeitlichen Unterschiede. Dennoch wurde bei einigen Arten eine geringfügige Änderung der Vertikalverteilung beobachtet, die aber als nächtliche Dispersion interpretiert werden kann.

Die morphologische Entwicklung von zwei der häufigsten Arten der Bucht wurde detailliert beschrieben. Die Entwicklungsreihe von *Normanichthys crockeri* (Publikation III) und *Prolatilus jugularis* (Publikation IV) konnte für Individuen (frisch geschlüpft bis kurz vor dem Juvenilstadium) anhand von morphologischen Eigenschaften und Pigmentierungsmustern verfolgt werden (Veröffentlichung III und IV). Insgesamt konnten 5.387 Larven (5.155 bzw. 232 Larven für *N. crockeri* und *P. jugularis*) identifiziert werden. Die Ontogenese beider Arten wurde beschrieben und illustriert, sie basiert auf insgesamt 104 Exemplaren (66 bzw. 40 Individuen jeder Art) mit einer Körperlänge zwischen 1,9 und 25,9 mm (frisch geschlüpfte Larven bis hin zu Larven im Transformationsstadium). Die Larvenschlupfgröße, Informationen zu den verschiedenen Stadien (“preflexion”, “flexion”, “postflexion” and “transformation”), Haupteigenschaften für die Bestimmung der Larven und meristische Informationen einschließlich Flossenstrahlberechnungen wurden genau beschrieben. Zudem wurden einige osteologische Analysen für *Normanichthys crockeri* durchgeführt (Veröffentlichung III). Basierend auf Pigmentierung und morphologischen Eigenschaften wurden insgesamt 49 Larven, die mindestens bis auf Familien-Niveau bestimmt wurden, gezeichnet (Publikation III, IV, Anhang 6). Die Abbildungen dienen als Bestandsliste des in der Independencia-Bucht vorkommenden Ichthyoplanktons und sollen für die Erstellung eines Bestimmungsschlüssels für das Ichthyoplankton dieses Gebiets verwendet werden.

RESUMEN

Este estudio está enfocado en la identificación, dinámica de ensamblaje y patrones de distribución de larvas de peces en la Bahía de Independencia, Pisco, Perú. Con el objetivo de definir la estructura de la comunidad de larvas de peces en la Bahía, se usó una combinación de técnicas de análisis univariado y multivariado. Basándose en muestreos mensuales de plancton realizados en el año 2000, se determina la composición, abundancia y estacionalidad del ictioplancton en la Bahía (Publicación I), se definen los patrones de abundancia en un ciclo de 24 horas y su relación con los parámetros medioambientales y se determinan las variaciones verticales de las familias dominantes en el área (Publicación II) con lo que se evalúa la función de la Bahía como sitio de desove y cría para los principales grupos de peces - y se describe además el desarrollo morfológico de algunos grupos de ictioplancton del área.

Se capturaron en total 16.156 larvas pertenecientes a 34 familias, 48 géneros y 48 especies. Las familias Engraulidae, Normanichthyidae, Blenniidae, Gobiesoscidae, Haemulidae, Labrisomidae, Pinguipedidae y Atherinidae dominaron la diversa ictiofauna, representando el 96.8% de las larvas capturadas; el 3.2% restante incluye varias familias. Los promedios mensuales de la densidad total de larvas de peces mostraron dos máximos: uno en primavera, dominado por larvas recién eclosioandas de " Mote" o "Camotillo" (Normanichthyidae) y de "Anchovetas" (Engraulidae), estas últimas en estado de preflexión; y un segundo pico (más pequeño) en el verano dominado por "Anchovetas" en estado de preflexión, seguidas por "Mote" o "Camotillo". Los promedios mayores de densidad larval se registraron entre septiembre y noviembre, lo cual sugiere un período principal de desove. En el mes de octubre se registró el promedio más alto de densidad de larvas de peces, alcanzando un valor de 7.492 larvas/100 m^3. Durante el verano, la mayor densidad promedio de larvas se registró en el mes de febrero (2.493 larvas/100 m^3). En lo que respecta a los valores totales de abundancia larval, no se encontraron diferencias estadísticamente significativas entre las estaciones. En octubre (primavera austral), la abundancia en Santa Rosa fue más alta que en Tunga, Pampa o Panteón. Pero en Febrero (verano austral), por el contrario, la abundancia en esas tres ultimas estaciones fue más alta que en Santa Rosa. Los máximos de abundancia de larvas de peces de la primavera y el verano coincidieron con altos "stocks" de zooplancton en la zona, y también (aproximadamente) con períodos de máxima surgencia. En general, la presencia de elevadas densidades de larvas de peces y el amplio rango de estadíos larvales permiten sugerir que la Bahía de Independencia sea un sitio regionalmente importante para el desove y la cría de peces marinos. El análisis de componentes principales (PCA) mostró que la temperatura y la salinidad explican la mayor

fracción (74.4%) en la variabilidad de los patrones de ensamblaje observados. Las condiciones medioambientales presentaron variación en el tiempo, entre estaciones y entre profundidades, sin embargo, no se pudo identificar algún término claro de interacción. El modelo logístico multinomial mostró que el ensamblaje de larvas y los parámetros medioambientales estabán asociados de un modo complejo.

Se examinaron los patrones de distribución vertical del ictioplancton de la Bahía basados en datos de dos profundidades y en solo dos de las cuatro estaciones. Blenniidae, Engraulidae, Gobiesocidae, Normanichthyidae, Atherinidae, y Labrisomidae dominaron numéricamente la diversidad de la ictiofauna en Panteón - cerca de Isla La Vieja - y representaron el 97.6% de las larvas capturadas. Gobiesocidae, Atherinidae, Pinguipedidae, Blenniidae, Engraulidae, y Labrisomidae fueron las familias más abundantes en Tunga - cerca de la costa - y conformaron el 77.6% de las larvas capturadas. La mayor densidad larval y mayor abundancia en la columna de agua se encontró en Panteón. El número de taxones fué el mismo (5) en la superficie de ambas estaciones, y fué mayor a media agua en Tunga (26) que en Panteón (21). Se observaron dos patrones verticales de distribución. Las larvas de la mayoría de las especies se localizaron principalmente en la capa media de agua (10 m), *Odontesthes regia regia* se encontró principalmente en la superficie. No hubo diferencias estadísticamente significativas entre las densidades diurnas y nocturnas en ninguna de las dos profundidades. Sin embargo, fué detectado un pequeño grado de redistribución vertical para algunas de las especies, lo que podría ser interpretado como una dispersión nocturna.

Se hizo una descripción detallada del desarrollo morfológico de dos de las especies dominantes de la Bahía. Basándose en características morfológicas y patrones de pigmentación de los individuos, se presentan diferentes series de desarrollo larval (desde recién eclosionados hasta metamorfosis) para dos especies: *Normanichthys crockeri* (Publicación III) y *Prolatilus jugularis* (Publicación IV). Se identificaron un total de 5,387 larvas (5,155 y 232 larvas para *N. crockeri* y *P. jugularis* respectivamente). La ontogenia de ambas especies se describió y se ilustró con base en un total de 104 especímenes (66 y 40 individuos para *N. crockeri* y *P. jugularis* respectivamente) que variaron en tamaño entre 1.9 y 25.9 mm: larvas recién eclosionadas hasta estadío de transformación o metamorfosis. Se presenta información referente al tamaño de eclosión de las especies, información referente a los diferentes estadíos (preflexión, flexión, postflexión y metamorfosis), las características principales para identificar dichas larvas y se da la información merística pertinente, incluyendo conteo de radios de las aletas. Se hizo también un análisis osteológico completo para *N. crockeri* (Publicación III). Se ilustraron un total de 49 especímenes (ver publicaciones III, IV, y Apéndice 6), donde se muestran características morfológicas y de

pigmentación de las larvas de Bahía Independencia. Esas ilustraciones serán usadas para completar una guía de ictioplancton para la región (*en preparación*), la cual será complementada con información ecológica y merística.

1. INTRODUCTION

1.1 General aspects

Knowledge of the natural history and ecology of fish larvae is essential to understand fish biology in general. The habitats, food sources and behavioral patterns of fish larvae may be so different from those of the adults, that the two can be considered as distinct eco-species. Fish larvae are difficult to identify because they may show very different morphologies to the adult fish, and this is a major reason why so little is known of the biology of fish larvae. In fact, some larval forms have been placed in a different family from the adults, or described as new genera (Leis and Trnski, 1989).

1.2 Coastal upwelling systems

Upwelling is a coastal process whereby cold, nutrient-rich bottom water is brought to the surface. Upwelling causes high productivity leading to large quantities of fish. Coastal upwelling areas are the sites of about 20% of global fish production, an amount far greater than would be expected on the basis of the 1% of the oceans' surface area that they occupy (Ryther, 1969; Cushing, 1971; Mann, 2000). Productivity varies between these upwelling systems as well as spatially within each, and also from year to year, in response to variations in wind strength, bathymetry, latitude, and the hydrographic properties of the water column (Botsford et al., 2003). However, quantitative understanding of how each of these factors contributes to production is still a subject of research. Upwelling occurs in some coastal regions, especially on the eastern sides of the Atlantic and Pacific oceans, but it can also be found in the open ocean, for example along the Equator. Coastal upwelling is known to occur on the west coasts of North and South America (California and Humboldt Currents, respectively), west Africa (Canary Current, Guinea Current and Benguela Current), and north east Africa (Somali Current). These are all areas of great biological productivity (Fig. 1). Upwelling zones are 66,000 times more productive than the ocean per unit area in terms of fish yield (Richards, 1981). Some aspects of coastal upwelling are dependent on the local combination of dynamic characteristics (e.g., variability of winds or river discharge), physical characteristics (e.g., shoreline irregularities or shelf width), and biological characteristics (e.g., availability of phytoplankton seed stock, structure of zooplankton communities, or functioning of the microbial loop) (Boje and Tomczak, 1978; Richards, 1981).

1.2.1 The Peruvian-Chilean upwelling system of the Humboldt Current

One of the world wide most productive fishing areas lies off the coasts of Chile, Peru and Ecuador (Fahrbach et al., 1980, Arntz et al., 1991). Strong coastal upwelling in this region results from moderately deep (50-100 m) water forced to the surface as a compensation for

surface water driven offshore by the combined effect of trade winds, the Coriolis force and Ekman transport, bringing nutrient-rich, cool water to the surface (Arntz and Fahrbach, 1991). The phytoplankton that thrives within this upwelling zone is fed upon by a variety of creatures including fish larvae. The biomass feeds an important food web that culminates in predatory fish, guano birds, and mammals (Mendo, 1997). The Peruvian upwelling occurs in a 300 x 300 mile area adjacent to the coast and is the most biologically productive example of a costal upwelling ecosystem on earth. The Peru-Chile or Humboldt Current is an Eastern Boundary current formed by a combination of the prevailing winds and currents of the south Pacific and the rotation of the earth. This current system extends from the south of Chile to the coastlines of Peru and Ecuador. Carbon levels in this upwelling region are tens of times higher than those of the next most productive upwelling region, the California current or the Benguela current (Arntz and Fahrbach, 1991).

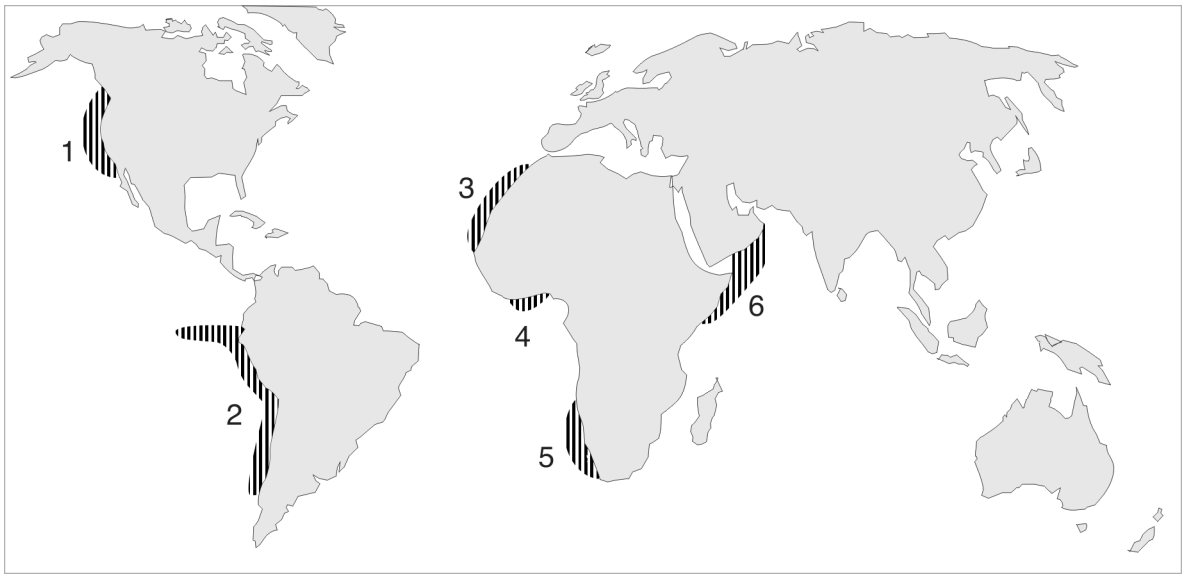

Fig.1. Principal coastal upwelling areas of high productivity in the world ocean. 1=California Current; 2=Humboldt Current; 3=Canary Current; 4=Guinea Upwelling; 5=Benguela Current; 6=North-east Monsoon Current (modified from Laudien, 2002).

1.3 El Niño impact on the ecosystem

An interannual variability termed the El Niño Southern Oscillation (ENSO) influences oceanographic conditions along the Peruvian coast. ENSO is characterized by a cold period (termed La Niña) and a period of anomalous warming in the eastern Pacific (El Niño) (Tarazona and Arntz, 2001), lasting between some months and various years (Arntz, *pers. comm.*). El Niño recurs irregularly with a period of 2-7 years. During El Niño events, the pycnocline deepens, and the transport of nutrient-rich waters into the euphotic zone is inhibited to such a degree that primary production may decrease by 50% (Chávez et al., 1989; Barber et al., 1985). The Peruvian upwelling system is thus perturbed by the arrival of

Kelvin waves, surface temperature rise, deepening of the thermocline, alteration of currents, reduced nutrient transport, an increase in dissolved oxygen at the sea floor, and increased H_2S reduction in sediments (Wyrtki, 1982; Arntz, 1986; Arntz and Tarazona, 1990; Arntz and Fahrbach, 1991; Jaimes, 1999). The month of occurrence, distance from the equator, water depth and the severity and duration of the individual event determine the local effects seen in an El Niño year. Species distribution changes in response to El Niño events, e.g. with species migrating away from the Panamanian province to the ocean off northern Chile. Changes of pelagic fish populations occur in other upwelling systems that are unaffected by ENSO, due to global climatic changes, and similar effects might also be expected to be seen in the observations made off Peru. The regional economy is strongly affected by ENSO as well, because it has direct impacts, both positive and negative, on a number of commercially exploited species, and their reproduction and early stages. ENSO effects are often difficult to distinguish from the decadal-scale impact of the Pacific Decadal Oscillation (PDO) (Francis and Hare, 1994; Francis et al., 1998).

1.4 Why studying ichthyoplankton?

Fish eggs and larvae (as well as some juveniles and adults - e.g., family Schindleriidae (*Schindleria brevipinguis, S. pietschmanni, S. praematura*) - that have a larval-like appearance as adults and are collected in plankton nets) are the vertebrates' contribution to the marine zooplankton and are collectively referred to as ichthyoplankton. The most abundant life stages of fish found in plankton are the eggs and larvae. As a percentage of the total plankton, the share of fish eggs and larvae is generally quite low, less than 5% in number and volume (Richards, 1985). However, at times they may be very abundant, as high as 100,000 under 100 m^2 of sea surface (Sherman et al., 1983). The information that may be obtained from ichthyoplankton is very important to ichthyologists, fishery biologists and managers of fisheries. It helps to determine the location of spawning grounds in space and time, the habitats used (and required) by fish during their larval phase, and fishery-independent estimates of stock size and stock boundaries. It is as well useful in the discovery of new fisheries, studies of the feeding habitats of larvae, their condition, and recruitment fluctuations (Leis and McGrouther 1994). This information provides a measure of ichthyoplankton importance in the ecosystem as prey, predators, and grazers (Hempel, 1974).

Ichthyoplankton specimens can also be used to investigate systematic relationships (Moser and Ahlstrom, 1974). The major prerequisite for utilizing ichthyoplankton is the identification of the eggs and larvae. It is estimated that there are about 22,000 species of fish, of which more than 13,000 are marine (Nelson, 1984). In viewing the overall knowledge of

identification, considerable progress has been made, but tremendous gaps do remain (Richards, 1985).

1.5 Early life history stages (ELHS)

Early life history stages (ELHS) of marine animals are critical in determining the status of adult populations, as most species produce large numbers of eggs and larvae that are cast into the sea to spend days, weeks, months, and even years (e.g., Dover sole *Microstomus pacificus,* family Pleuronectidae, that has a pelagic larval period lasting from 1 to 3 years (Toole, et al.,1993; Buttler et al., 1996)). Larvae develop and juveniles mature sometimes far from the site of the adult habitat. These ELHS are pelagic or demersal and may drift with currents over wide distances. The proportion of fish that spawn planktonic eggs tends to vary as a function of latitude: the lower the latitude the higher the proportion with planktonic eggs. Planktonic stages potentially can be dispersed over large distances, depending on their duration, the local flow regime, and whether larvae develop behaviors (e. g., vertical migration) to reduce dispersal. Larvae that hatch from demersal eggs, or larvae of live-bearers are typically better developed and commonly larger at hatching than larvae that hatch from planktonic eggs, and they tend to be less susceptible to dispersal (Watson, pers. comm). Eventually, late larvae or early juveniles return to nursery areas near adult habitats. This whole process is very complex and dynamic with many external events controlling populations (Lasker, 1981; Richards and Lindeman, 1987; Anderson, 1988; Cushing, 1990; Horne and Smith, 1997). Between spawning and recruitment into the adult population, most fishes undergo dramatic changes in morphology. The most general scheme of terminology for the early development of fishes includes the following: (1) The “egg stage” (spawning to hatching). The egg stage (Fig. 2) is used in preference to the embryonic stage because there are characters present during this stage other than just embryonic characters (e.g., those associated with the egg envelope). (2) The “larval stage” (hatching to attainment of complete fin ray counts and beginning of squamation). One of the fundamental events in the development of most fishes is the flexion of the nothocord that accompanies the hypochordial development of the homocercal caudal fin. It is convenient to divide the larval stage on this basis into “preflexion”, “flexion”, and “postflexion” stages (Appendix 1). The early life history of fish has been and continues to be studied from a number of different perspectives (Ahlstrom and

Fig. 2. Eggs and larvae of *Engraulis ringens.*

Moser, 1976). Historically, several disciplines have used different names for the same stage, or subdivided development differently (see Okiyama, 1979 and Appendix 2). Some anatomical and morphometric features of the early stages of fishes are shown in appendices 3 and 4.

1.6 Ichthyoplankton and related studies in Peru

Coastal regions are important nursery grounds for littoral and shelf fish populations, with shallow areas offering suitable food supply, shelter, and ecophysiological conditions for development of all stages from eggs to juveniles (Blaber and Blaber, 1980). It is well documented that many populations of coastal fish depend on such critical areas, at least during part of their life cycle (Weinstein, 1979; McHugh, 1985).

Peru contains a rich fish fauna with more than 1000 species (Chirichigno and Cornejo, 2001). Literature pertaining to adults of marine teleost fish species throughout Peru was started in 1833 by European scientists (Chirichigno and Vélez, 1998). The most complete work was done by Hildebrand (1946), who described 261 species. Koepcke (1951) published an identification key for 100 coastal species, and Chirichigno (1974) published an identification key that included 566 species. Vélez (1980) published an identification key with 83 species from the central coast of Peru. In 1998, Chirichigno published a second version of her book from 1974 and presented 727 species from 388 genera and 138 families, the most complete key for the identification of adult marine fish in Peru. Chirichigno and Cornejo (2001) listed 1,070 species, 549 genera, 194 families and 39 orders of marine fish in Peruvian waters. Published information describing larvae of Peruvian fishes is poor and sparse, and has been until now restricted to a few publications on larval development of a small number of species (e.g. Einarson and Mendiola, 1963; Chirinos de Vildoso and Chumán, 1964; Santander and Castillo, 1969, 1971; Guzmán and Ayón, 1995; Vélez et al., 2003a, 2003b).

According to Guzmán and Ayón (*pers. comm.*), only some larval descriptions (24 species, and 34 genera) of Peruvian fishes have been published, representing a low percentage (2.2% and 6.2%, respectively) of the Peruvian fish fauna known or described as larvae (Appendix 5). Furthermore, the knowledge of the ichthyoplankton and its ecology is still limited (e. g. Richards, 1985) and this is especially true for the Pacific coast of South America. Marine fish diversity is high in Peruvian waters, but the larval stages are poorly known (e.g. Vélez et al., 2003b). The lack of ichthyoplankton information for Peru is even more evident when compared with the knowledge of ichthyoplankton in other geographical areas. Although regional guides to ELHS of fishes are available for many large areas of the world ocean (Kendall and Matarese, 1994), such guides are noticeably lacking for both

coasts of South America, as are guides to most oceanic regions. Despite the importance of knowing the processes affecting the dynamics of the coastal ichthyoplankton, most of the ichthyoplankton studies carried out in Peru have focused on mesoscale surveys over the continental shelf and have concentrated on fish with commercial value (Guzmán and Ayón, 1995; Guzmán and Carrasco, 1996). To date, no scientific information is available on the ecology of ichthyoplankton in Independencia Bay, although it is an area of upwelling and possibly an important spawning and nursery area. It is important to increase our ecological knowledge of Independencia Bay because, as with the entire Pacific basin, it is affected by developments that are tied to major economic activities of fisheries. A study of the distribution patterns of fish larvae contributes to an understanding of the interrelationships among fishes during their early life stages, as well as to an understanding of adult spawning patterns.

1.7 Objectives of this study

The focus of this study is on describing ichthyoplankton in Independencia Bay, and on assessing what factors could influence fish larvae there. To accomplish this, I studied aspects of the ecology of the fish larvae in Independencia Bay, with emphasis on the influence of oceanographic processes on ELHS. In particular, to assess the inferred function of the bay as a spawning and nursery ground for marine fish in the region, the objectives of this thesis are:

(1) To assess the seasonal variations of the dominant families during an annual cycle.
(2) To determine diel abundance patterns, assess the vertical variations of the dominant families in the area during a 24-hour cycle and relate these variations to oceanographic parameters.
(3) To establish the taxonomic composition of fish larvae in Independencia Bay.
(4) To provide a description of development from just after hatching through transformation to the juvenile stage for some species to facilitate identification of these species in ichthyoplankton samples.

2. STUDY AREA

2.1 General Information

Independencia Bay (14º06'-14º20'S; 76º00'-76º18'W) is a large, shallow bay situated within the Paracas National Park, Pisco, Peru. (Fig. 3). Paracas National Reserve is located along the Pacific coast, on the Peninsula and Bay of Paracas, 265 kilometers south of Lima, in the Province of Pisco; it is the only protected coastal-marine system in Peru. The Paracas National Reserve (335 thousand hectares) is an ideal example of the Pacific subtropical coastal desert zone; 65% of the reserve is in marine waters and the remaining 35% is mainland. It is located in the Humboldt Current Marine Ecoregion and is a marine upwelling site, with high levels of primary production (Vélez et al., 2004a). With its high diversity and abundance of marine resources, it is considered as a rich ecosystem in Peru. Independencia Bay is ca. 21 km long and 6.5 km wide, with an irregular sea-floor topography, and a variety of habitats including seagrass meadows, sandy and rocky floors that provide spawning and nursery areas for a wide variety of marine organisms. Tidal mixing with open coastal water and the high run-off of nutrients from guano bird colonies at La Vieja are main factors leading to high primary production in the bay, resulting in high biomasses in the area (Tarazona et al., 1989). Much of the bay is 22-25 m deep, with the deepest point at La Trujillera (85 m), and the shallowest point (7-18m) north of Independencia or La Vieja Island. There are two islands, La Vieja and Santa Rosa. La Vieja island (5.6 km long and 2.4 km wide) occupies most of the southern half of the mouth of the bay, and is oriented in the same direction as the coast. The coast of La Vieja is abrupt and its slope is steep.

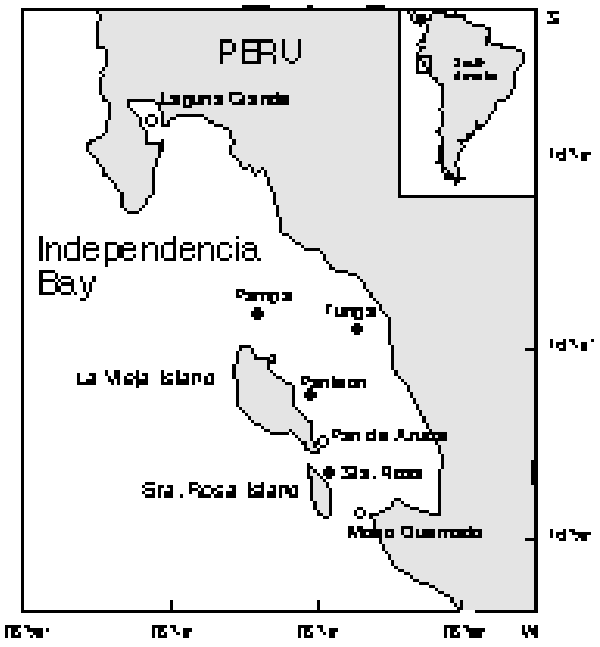

Fig. 3. Study area, Independencia Bay, Pisco, Peru. Sampling locations indicated by black points. Black points=main stations (standard sampling); white points=extra stations (additional sampling).

2.2 Artisanal fisheries

Shallow South American waters (i.e. <40 m) are well supplied with oxygen except in protected zones such as Independencia Bay – the most important area for artisanal bivalve fisheries in Peru – where oxygen concentration may fall at depths below 10 m. However,

A

B

Fig. 4. La Vieja island (A) and Coast of Independencia Bay (B), Pisco, Peru.

wind and wave action, as well as the high density of seaweeds, increase oxygen supply. Thus, the well-oxygenated shallow water zone off Peru and northern Chile where seafood (particularly molluscs and crustaceans) is caught by artisanal fishermen, typically extends to depths of 15 to 40 m. This narrow coastal strip is extraordinarily rich in nutrients and plays a very important economical role. Earlier, between 1983 and 1984 there were some 5000 boats working in these shallow Peruvian waters (Arntz and Fahrbach, 1991). More recently, Mendo (1997) reported that artisanal fisheries employ 600 fishermen and in total 20.000 people. Even today, a great number of artisanal fishermen work directly on the coast, and thousands of people are responsible for processing, transportation and selling of catches. The catches officially taken through artisanal fisheries are much higher than those obtained through deeper water trawling. There are probably many other unreported (i.e. subsistence fishery) catches (Arntz and Fahrbach, 1991).

2.2.1 The prosperity of the scallop *Argopecten purpuratus*

During the Niño period 1982-1985, the scallop harvest in Independencia Bay was the highest in recorded Peruvian history, and during El Niño 1997-1998, this resource was also favoured by the warm water condition but, as a result of stock mismanagement, the harvest was much lower than during the previous El Niño 1982-1983 (Wolff and Mendo, 2000). During 1982-1983, the scallop *A. purpuratus* and a few other local species showed a massive development (Arntz and Fahrbach, 1991). Under normal conditions, these organisms, particularly the snail *Thais chocolata* and the octopus *Octopus mimus* are found in relatively low densities. They are thus normally caught with other invertebrates. These organisms, contrary to most other invertebrate species, share a higher tolerance to high temperatures and proliferate under the increased temperatures during El Niño, when the oxygen supply is high and primary production in the shallow waters is relatively high, in contrast to the pelagic zone of the open ocean (Tarazona, *pers. comm*.). Competition between species is reduced during El Niño, due to the mortality of benthic competitors. The prosperity of the Peruvian scallops began with the special recruitment during El Niño in 1983. The scallops, which normally live in more than 20 m of water, extended their habitat in the Paracas Bay (South of Pisco) to waters between 6 and 10 m. They reached their commercial size within 6 months (Arntz and Fahrbach, 1991). The population was about 60 times bigger than in normal years with more than 100 individuals per 100 m^2 and a biomass of 5-8 kg per m^2. In a short period, many divers and boats were attracted to the Paracas Bay area for the richness of its resources. In Pisco, many companies started with processing of the scallops and in the second season of 1983, 20 tons of adductor muscles from *A. purpuratus* were exported to the U.S.A. (Arntz and Fahrbach, 1991).

2.3 Oceanography

The oceanographic characteristics of Independencia Bay are influenced by the Humboldt Current, which flows northwards along the west coast of South America from southern Chile. The hydrography of the shelf area off Peru is dominated by two main currents: The Humboldt Current (PC) and the Humboldt Countercurrent (PCC), both of which are involved in the upwelling process. The PC flows along the surface in a northerly direction, while beneath it the PCC flows southwards as an undercurrent. In the following, the PCC will be termed the undercurrent, or UC. The mean velocities of both currents are approximately 20 km/day (Barber and Smith, 1981). The PC is about 20 km wide and its main flow path lies 50-70 km from the coast. The subsurface UC, which is supplied by near-surface waters of the Equatorial Counter Current, flows from 5°S to 20°S, at a depth of 50-100 m. However, due to the coastal morphology, the UC can reach water depths of 300 m in some places (Brink et al.,1983).

2.4 Oxygen minimum zone

An oxygen minimum zone (OMZ) exists on the Peruvian shelf (Brockman et al., 1980), within which the oxygen content of the water and sediment does not exceed 0.5 ml/l (Rosenberg et al., 1983, Mullins et al., 1985). The central portion of the Peruvian OMZ is distinguished by an oxygen content of <0.2 ml/l and lies between 100 and 400 m water depth (Burnett et al., 1980). The average oxygen content of the bottom water in the area is assumed to be <0.3 ml/l (Summerhayes et al., 1992; Tarazona and Arntz, 2001). Dissolved superficial oxygen concentrations off the Peruvian coast vary in the range 2-7 ml/l. Off the central Peruvian coast, oxygen minima (<0.5 ml/l) and frequent anoxia occur mostly between 50 and 700 m depth, owing to high organic matter accumulation and microbial activity (Rowe, 1985). However, low oxygen values may also be associated with shallow depths (<20 m) in protected bays (Tarazona et al., 1991). Although oxygen concentrations at the sea floor tend to diminish from north to south, below the OMZ they rapidly increase with depth. Owing to an influx of equatorial water, dissolved oxygen values increase strongly during El Niño events (Arntz et al., 1991) and, on the whole, dissolved oxygen concentrations seem to be the principal selective factor for the benthic, demersal, and pelagic invertebrate and fish fauna on the continental shelf off Peru.

3. MATERIAL AND METHODS

3.1 Sample collection

Larvae were collected monthly during January-May, and August-November in the year 2000 (Table 1). March-April was combined as one sampling period, these samples were taken between the end of March and beginning of April. Plankton was collected with two net types: a 60 cm Bongo net equipped with 0.505 mm and 0.333 mm nitex mesh nets and cod ends, towed at a depth of 10 m, and a half-meter ring net (0.333 mm nitex mesh) towed at the surface. Both nets were equipped with calibrated flowmeters. All tows were taken at a speed of about 1.5 m/s for 10 min. and samples were preserved in 4% formalin solution immediately after collection. A total of 64 horizontal tows was made at daytime (between 08:30 and 14:00) at four stations (Santa Rosa, Panteón, Tunga, Pampa) (Fig. 1). Furthermore, 37 additional samples (Table 1, Publication I) were included in a compositional analysis of the ichthyoplankton, but were not used for distributional analysis. The additional tows were made in September; one daytime sample was taken at three stations (Morro Quemado, Pan de Azúcar, Laguna Grande), at Panteón, two additional daytime samples were taken. At Panteón and Tunga, a total of 32 horizontal tows were made (Publication II), here each station was sampled every three hours during a 24 hour period. All sampling was done during two 24-hour cycles.

Table 1: General information of the sampling in Independencia Bay in 2000. Temp=Temperature, 1=Standard net, 2=Bongo net

Station	Position	Depth (m)	Tows 0m	Temp 0m	Tows 10 m	Temp 10m	Net	Sampling period
Standard sampling								
Pampa	14°24' S-76°11'W	23	8	14.4-20.3	8	13.9-15.7	1,2	All year
Tunga	14°14'S-76°08'W	21	8	14.4-19.1	8	13.5-17.0	1,2	All year
Panteón	14°17'S-76°17'W	20	8	14.0-17.1	8	13.7-16.9	1,2	All year
Santa Rosa	14°19'S-76°09'W	27	8	13.7-16.9	8	13.4-15.8	1,2	All year
Additional sampling								
Panteón-24 H	14°17'S-76°17'W	20	8	13.8-14.5	8	13.7-14.1	1,2	September
Tunga-24H	14°14'S-76°08'W	21	8	13.6-15.4	8	13.5-14.5	1,2	September
Laguna Grande	14°09'S-76°14'W	10	-	14.7	1	14.4	2	September
Pan de Azúcar	14°18'S-76°09'W	14	-	14.9	1	14.6	2	September
Morro Quemado	14°40'S-76°30'W	15	-	14.4	1	14.3	2	September
Panteón	14°17'S-76°17'W	20	-	14.1	2	13.9	2	September

3.2 Abiotic parameters

Using a Niskin bottle, temperature, salinity, pH and dissolved oxygen were measured at four depths (0, 5, 10 and 20 m) during each collection at the four standard stations (Santa Rosa, Panteón, Tunga, Pampa). The physical data for the months of June, July and December were provided by Dr. J. Tarazona (Universidad Nacional Mayor de San Marcos, Lima, Peru). See Publication I and II for details. Upwelling index information for waters adjacent to Pisco

(15º S-77º W) was obtained from the Pacific Fisheries Environmental Laboratory-NOAA (http://orpheus.pfeg. noaa.gov/outgoing/upwell/SA/spac11.15s.mm),(Publication I). Tidal information for the Pisco area was obtained from tidal tables published by HIDRONAV-5023 (2000), (Publication II). Sunrise and sunset were determined for local Pacific Daylight Savings Time (PDST) from the nautical atlas (Publication II).

3.3 Zooplankton biomass

In the laboratory, zooplankton biomass was measured from each sample using the displacement volume method (Beers, 1976) (Publications I and II).

3.4 Treatment and data analysis

Because some specimens could not be identified to genus or species level, abundance data were summed at the family level in the quantitative analyses. Fish from the most abundant families in this study were identifiable to species level. Numbers of fish larvae in each tow were standardized to the number per 100 m^3 of water filtered. Univariate and/or multivariate analyses were used for publications I and II. Treatment of morphological data is presented in detail in Publication III and IV. For a more detailed description of each analysis used, see the respective publications.

3.4.1 Statistics

A multivariate ANOVA (Publication I) was used to test for differences in the vector of environmental variables over time, station and depth. Three test statistics were considered for this purpose (Wilk's lambda, Pillai's trace and the Hotelling-Lawley trace), each of which measures specific aspects of the multivariate distances. In order to avoid conclusions on the basis of ambiguous decisions, an effect was considered as present only if all three test statistics produced a significant result. Pairwise comparisons between months, stations and depths were performed by multivariate contrasts with Bonferroni correction. Here, all three previously mentioned statistics coincide, because only two groups are compared. Unless stated otherwise, an α error of 0.05 was used in statistical tests. To determine whether the seasonal abundance changes of larvae of the most common families were statistically significant, Poisson regressions (McCullagh and Nelder, 1989) using the number of fish larvae and volume of water filtered per tow were performed on untransformed count data, with months and stations as classification factors. These procedures were run in the GLM (General Linear Model) Module of SAS (SAS, 2001). The relations between species assemblage and environmental variables were analyzed by a multinomial logistic model (McCullagh and Nelder, 1989), using the LOGISTIC module of SAS (2001). In Publication II, densities (larvae/100 m^3) of the seven most abundant taxa (total number of larvae >90) were

tested. Data were also transformed to log (x+1) prior to testing. All statistical analyses were based on catches in the 0.333 mm mesh samples from both depths. The null hypothesis, of no differences among stations or strata, was evaluated at a significance level of $p \leq 0.05$. I used a three-factor analysis of variance (ANOVA) with the following factors: Station (Panteón vs Tunga), depth (surface vs 10 meters), and time (day vs night). A Friedman test and the Student-Neuman-Keuls (SNK) test were used for differences in abundance of larvae between stations. Differences in concentration of larvae between depths, and between day and night were detected in a similar manner. The PC-ORD for Windows (McCune and Mefford, 1999) was used for a canonical correspondence analysis (CCA) (Ter Braak, 1986). The CCA was used to examine the relationships of variations in density of the dominant species and environmental variables.

3.4.2 Multivariate analysis

Multivariate analyses (Publication I), based on the dominant species collected with the Bongo and surface nets (0.333 mm mesh, only), were used to examine temporal (seasonal) and spatial (vertical dimension) patterns of the larval fish assemblages. To further examine temporal patterns and to calculate the similarities between stations and taxa, the Bray-Curtis dissimilarity coefficient was calculated using log (x+1) transformed standardized abundances for each month, station, season of the year, and for each depth (Surface and 10 m) where the samples were taken (Publication I). The log (x+1) transformation was used to reduce the contribution from numerically dominant species and to reveal changes among less dominant species (Field et al. 1982). Abundances of taxa were summarized in separate matrices for each factor analyzed; only the eight most abundant taxa were included. A classification (cluster analysis, complete linkage) of the similarity matrices was made for all stations and taxa. Non-metric multidimensional scaling (MDS) was used to graphically display two-dimensional ordination plots of the inter-relationships among samples, based on the relative abundance of each taxon. A low (<0.2) MDS stress coefficient indicates that the multivariate similarity pattern is represented by the plot without much distortion. The PRIMER program was used for these analyses (Clarke and Warwick, 1994).

3.5 Larval fish identification

Problems in the identification of early life history stages are very pronounced along the Peruvian coast, especially in Independencia Bay, where no previous study of ichthyoplankton has been made until now. Guzmán and Carrasco (1996) reviewed the work on ichthyoplankton and zooplankton of the Peruvian waters of the last three decades, and summarized in a concise way all the results of these investigations. They also present all the bibliographical references on ichthyoplankton and zooplankton separately.

In the laboratory, all fish larvae were sorted from the samples and identified to the lowest taxon possible. Larvae were identified by the series method (Moser, 1996; Leis and Carson-Ewart, 2000), using a combination of meristic and developmental characters that permitted definitive identification. I encountered some very difficult identification problems in this work. I could not identify all eggs from our samples because of the lack of complete developmental sequences and the sparsity of literature descriptions. In total, 99.6% of the fish larvae found in this study were identified to at least the family level.

Using morphological features and pigmentation, two complete larval development descriptions were made in this study (Publication III and IV). Totals of 5,387 larvae (5,155 and 232 larvae for *Normanichthys crockeri* and *Prolatilus jugularis*, respectively) were identified. The ontogenies of *N. crockeri* and *P. jugularis* were described and illustrated based on a total of 104 specimens (66 and 40 for each species, respectively) ranging from 1.9 to 25.9 mm in length: recently hatched larvae through transformation stage. I used only specimens in good condition, which were measured to the nearest 0.02 mm with the ocular micrometer of a dissecting microscope. Measurements were completed within 1.5 years after collection. Methods of counting and landmarks for measurements are defined by Moser (1996) and Leis and Carson-Ewart (2000). Body parts measured include: Body Length (BL), Snout-Anus Length (Sn-A), Body Depth (BD), Head Length (HL), Head Width (HW), Snout Length (SnL), Eye Diameter (ED), Pectoral Fin Length (P_1L) and Pelvic Fin Length (P_2L). Larval hatching sizes, information concerning the different stages (preflexion, flexion, postflexion and transforming), main diagnostic features, and meristic information including fin ray counts were given. In these descriptions, larval lengths always refer to body length. The morphometric series served as the basis for descriptions of the pigment pattern. Description of pigmentation refers solely to melanophores.

3.6 Illustrations

All the illustrations were made using a camera lucida attached to a dissecting microscope, thus assuring accurate proportions and pigment placement. A total of 49 specimens as illustrated (see Publications III, IV and Appendix 6) show pigmentation characters and some morphological features of the larvae found in Independencia Bay (most of them identified at least to the family level). The illustrations presented in Publication III and IV show a complete series of sizes and morphological changes to provide identification of all stages that document the development of both species described. The illustrations presented in Appendix 6 are the subject of a separate ichthyoplankton identification guide for the area (*in preparation*), which is not included here except for use in compiling the most complete

ichthyoplankton species list possible for the bay and for giving some graphical idea of the species found.

3.7 Systematics and taxonomy

Developmental and taxonomic studies are needed to document morphological development, ontogenetic events, and characters of diagnostic or systematic value. A number of techniques have been developed to help in the identification and classification of fish larvae.
Since the development of the skeleton and meristic characters are so important in identification, techniques of clearing and staining, x-radiography, rearing experiments and otolith morphology have been used. More recently, fluorescence and scanning-electron microscopy, computer-image measurement and analysis and PCR processing as well as m-DNA analysis have been used to enhance identification capabilities (Moser et al., 1984).

3.7.1 Clearing and staining

The clearing of tissues and the staining of cartilage and bone are useful in the study of larval and juvenile fishes. The technique works well for all sizes, with adjustments (Appendix 7) in the various solution soaking times made depending on fish size (Moser et al., 1984). Clearing and staining is a method of preparing skeletons that leaves flesh clear, bones red, and cartilage blue. This technique shows how bony the skeleton of the fish is. In this study, many specimens ranging from preflexion to late transformation stage were cleared with KOH and stained with Alizarin red-S, to observe ossification of the jaws, suspensorium and opercular series bones, axial skeleton, appendicular skeleton and fins (Publication III). Staining procedures followed Potthoff et al., (1984). Skeletal structures were considered ossified upon uptake of Alizarin red-S stain (see section 4.4.1.2).

3.7.2 X-ray

Radiography (Fig. 5) is useful for obtaining skeletal information in studies of fish taxonomy and morphology. Although clearing and staining provides more detail, radiography has other advantages. It produces an easily stored, long-term record of skeleton and does not permanently alter the condition of the specimen. In many cases, counts can be obtained more accurately from radiographs than from the specimens themselves (Tucker and Laroche, 1984). Radiography is also easier and faster than clearing and staining (Moser et al., 1984). In this study, radiography was done using a digital X-ray setup, which enables images to be edited and retrieved quickly. Many specimens (Publications III and IV) ranging from postflexion to adult were selected for radiography in order to obtain more accurate meristic counts. The numbers of dorsal- and anal-fin elements, and vertebrae were counted from radiographs of many specimens.

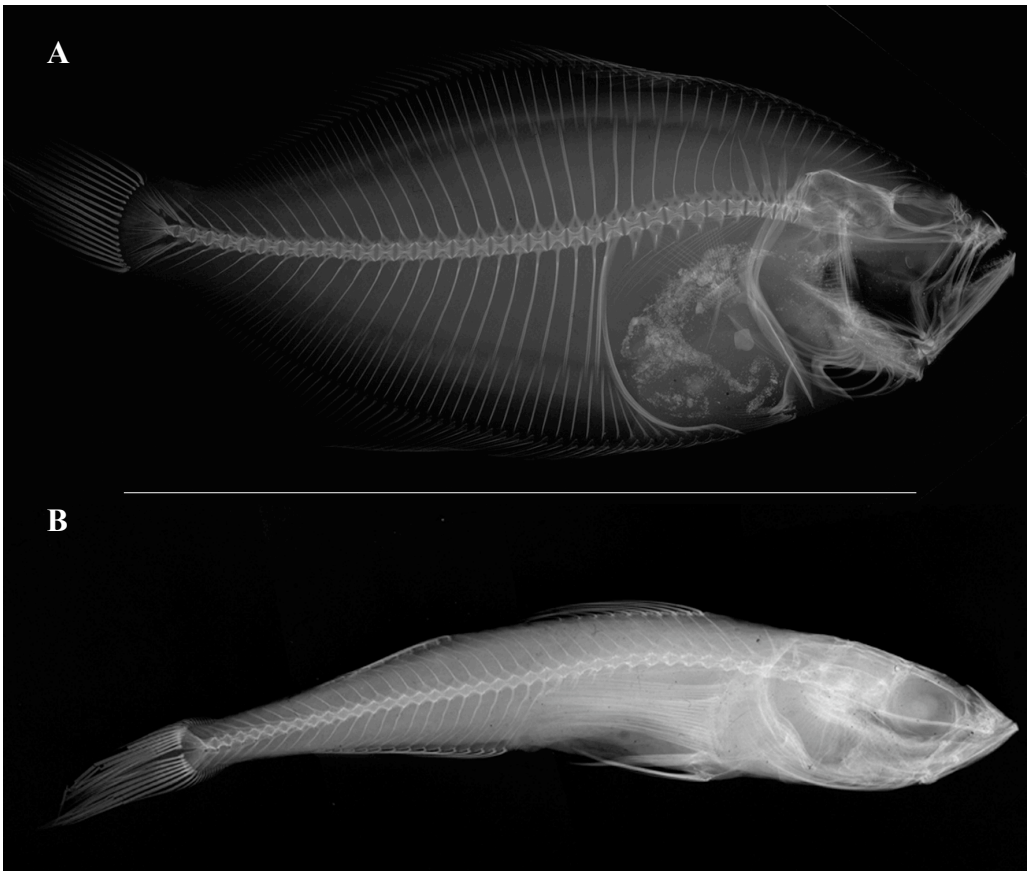

Fig. 5. Radiographs of adult fishes. (A)= *Paralichthys* sp.; (B)= *Prolatilus jugularis*.

4. PRINCIPAL RESULTS AND GENERAL DISCUSSION

In this chapter, the most important results (published and unpublished) are summarized and discussed. For additional details of results and further discussion see the attached publications. The first parts of this chapter (Sections 4.1, 4.2, and 4.3) focus on the structure of the larval fish assemblages in Independencia Bay. Temporal and spatial relationships (Publication I) and vertical distributions of the fish larvae (Publication II) are addressed. The fourth part of the chapter (section 4.4) presents taxonomic and systematic results and summarizes the morphological development of two of the more abundant species from the bay. Developmental series (recently hatched through transformation) of *Normanichthys crockeri* (Publication III) and *Prolatilus jugularis* (Publication IV) are presented, emphasizing morphological features and pigmentation patterns. A total of 49 specimens were illustrated (see publications III, IV, and Appendix 6). The illustrations show pigmentation and morphological features of the larvae from Independencia Bay, and will be used for a guide to the ichthyoplankton of the bay (*in preparation*), to be completed with ecological and meristic information. In the final part (section 4.5), some future perspectives will be outlined.

4.1 Structure of the larval fish assemblages in Independencia Bay

4.1.1 Taxonomic composition

In total, 16,156 fish larvae – representing 34 families, 48 genera, and 48 species – were collected. Twenty-nine families, 35 genera, and 36 species were identified (Table 2). Unidentified larvae contributed less than 1% of the total. The families Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae and Atherinidae numerically dominated the larval fish fauna in the bay and comprised 96.8% of the total larvae; the remaining 3.2% included several families (Table 2, Publication I).

Fish larvae from this study were divided into four groups on the basis of their adult habitat (Table 2): (I) inshore, benthic species; (II) inshore, neritic species; (III) coastal pelagic species that do not complete their life cycle exclusively in the bay; and (IV) epi- and mesopelagic oceanic species. Most of the members of groups I and II are common in Independencia Bay as adults (Reynaga and Mendo, 2002) and, as evidenced by these collections, spawn and probably complete their life cycles within the bay. The larvae of these two groups constituted > 66.6% of all larvae collected at all stations. Group III constituted 32.5% of the total larvae collected, of which 99.4% was constituted by *Engraulis ringens*. Group IV, the oceanic taxa, contributed less than 1% of the total larvae in the bay. The bay does not appear to be an important nursery area for the oceanic species, but it supports a

suite of inshore species and is likely to be a critical habitat area for them.

Table 2. Families of fish larvae grouped on the basis of their adult habitats reported in the literature (Nelson, 1994).Total number (N), percent contribution to all fish larvae caught (D= dominance), and frequency (F= % frequency) of capture of the ichthyoplankton taxa collected in Independencia Bay during the year 2000.

Family	Genus /Species	N	D	F	Family	Genus /Species	N	D	F
Group I					**Group II**				
Blenniidae	*Scartichthys* sp.	2898	18.0	86.7	Atherinidae	*Odontesthes regia regia*	218	1.3	53.3
	Hypsoblennius sp.	90	0.6	60.0	Centropomidae		1	<0.1	6.7
Chaenopsidae	*Emblemaria* sp.	2	<0.1	6.7	Haemulidae	*Anisotremus* sp.	329	2.0	53.3
Cheilodactylidae	*Cheilodactylus variegates*	1	<0.1	6.7	Labridae		2	<0.1	13.3
Ephippidae	*Parapsettus (panamensis?)*	1	<0.1	6.7	Normanichthyidae	*Normanichthys crockeri*	5155	31.9	80
Gerreidae	*Eugerres periche*	12	<0.1	13.3	Pomacentridae	*Chromis* sp.	9	<0.1	26.7
Gobiesocidae	*Gobiesox marmoratus*	1346	8.3	73.3		*Abudefduf (?)* sp.	1	<0.1	6.7
	Sicyases sanguineus	22	0.13	6.7	Sciaenidae	*Sciaena* sp.	4	<0.1	13.3
	Tomicodon petersi	2	<0.1	6.7					
Gobiidae	*Evermannia zostetura*	50	0.31	40.0	**Group III**				
Labrisomidae	*Labrisomus (philippii?)*	263	1.6	73.3	Clupeidae	*Sardinops sagax sagax*	7	<0.1	13.3
Ophidiidae		5	<0.1	13.3	Coryphaenidae	*Coryphaena hippurus*	2	<0.1	6.7
Paralichthyidae	*Paralichthys adspersus*	77	0.5	46.7	Engraulidae	*Engraulis ringens*	5225	32.3	93.3
	P. microps	12	<0.1	13.3	Kyphosidae	*Doydixodon* sp.	1	<0.1	6.7
	Etropus ectenes?	6	<0.1	6.7	Sphyraenidae	*Sphyraena idiastes*	1	<0.1	6.7
	Hippoglossina sp.	3	<0.1	13.3	Carangidae		3	<0.1	6.7
Pinguipedidae	*Prolatilus jugularis*	232	1.4	53.3					
Scorpaenidae	*Sebastes capensis*	12	<0.1	13.3	**Group IV**				
Serranidae		1	<0.1	26.7	Nomeidae	*Nomeus gronovii*	2	<0.1	13.3
Syngnathidae	*Leptonotus blainvillianus*	12	<0.1	6.7	Scombridae	*Auxis* sp.	3	<0.1	13.3

4.1.2 Spatial and temporal distribution

Most of the larvae collected in this study were in preflexion stage, which suggests that the bay may be an important spawning area, reflecting the spawning localities (i.e., inside or outside the bay) of adults. The monthly mean density of total fish larvae showed two peaks: one in spring (September-November), dominated by newly hatched mote sculpin (*N. crockeri*) and newly hatched and preflexion-stage anchoveta (*E. ringens*), and a smaller peak in summer, dominated by preflexion-stage anchoveta, followed by mote sculpin. The highest mean density of larvae (no./100 m^3) during the spring peak was 7,492 larvae/100 m^3, recorded in October. The greatest mean density during summer was recorded in February (2,493 larvae/100 m^3). The occurrence of high larval fish densities and the presence of older stages implies that the bay also serves to some degree as a nursery ground. Concerning the total larval abundance, there were no statistically significant differences between stations. The abundance in October (spring time) at Santa Rosa was higher than at the other three stations, but the abundance in those other 3 stations was higher in February (summer time), (Fig. 6).

Spawning of most of the abundant taxa probably occurs inside the bay. This includes *Engraulis ringens*, that is also known to spawn off the open coast (Gorbunova et al., 1985; Ayon, 2001a; 2001b; Girón, 2001). Both spring and summer ichthyoplankton abundance in Independencia Bay peaked in coincidence with the zooplankton volume and upwelling (Fig.

7). Hence, summer and early spring spawning in the bay may permit larvae to take advantage of the increased planktonic production at times of increased upwelling. Species composition differed between summer and spring, although the dominant species were present in both seasons, except for *Odontesthes regia regia* in summer and October. The reason for *O. regia regia*'s different seasonal spawning pattern is unclear, but its larvae are neustonic so that wind-driven surface transport may be an important factor in retaining larvae in the bay (Vélez, 2004a). Alternatively, some unknown adult spawning habitat requirement may be met only seasonally.

Most of the dominant species presented the main abundance peak between October and November (spring time). Only *Anisotremus* sp. presented a main abundance peak in February, and *Engraulis ringens* showed high peak abundances in both spring and summer time (Fig. 3, Publication I).

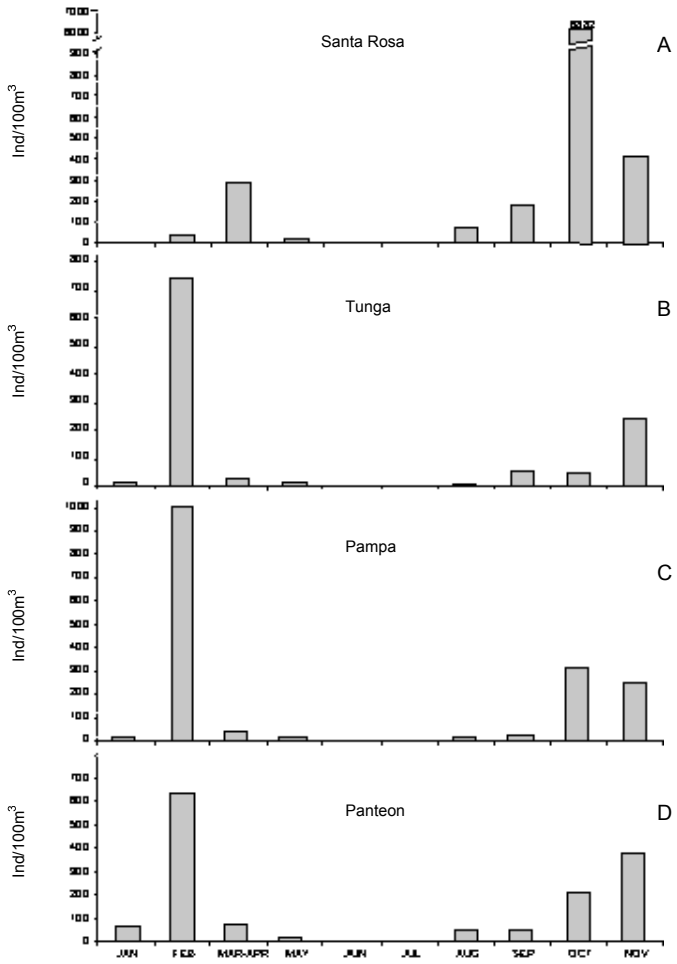

Fig. 6. Mean monthly density (No./100 m^3) of total larvae at the four stations sampled during the year 2000. Note the different abundance scales for the different stations.

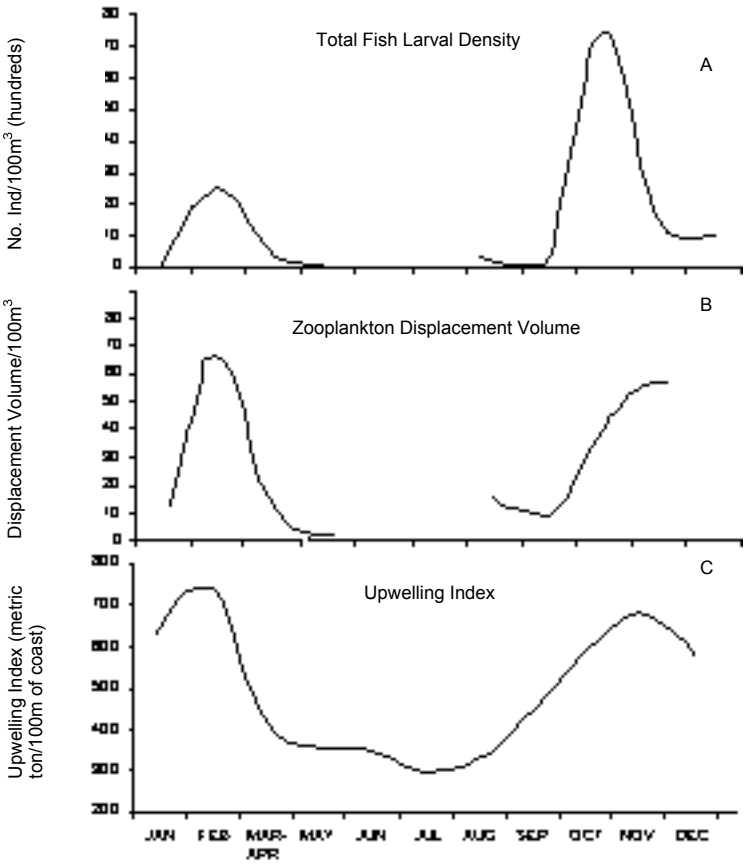

Fig. 7. (A) Total fish larval density (no./100 m^3), (B) zooplankton displacement volume (ml/sample) and (C) upwelling index (metric tons/sec/100 m of coast) during the year 2000. Upwelling index of waters adjacent to Pisco (15º S-77º W), from Pacific Fisheries Environmental Laboratory-NOAA (<ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/SA/spac 11.15s.mm>). Note that during June and July no samples were taken.

E. ringens is the most important Peruvian fisheries resource. A comparison of my results with results of IMARPE studies during 2000 (Ayón, 2001a; Girón, 2001) elsewhere on the Peruvian coast shows that larval abundances were generally of the same order of magnitude in the bay and off the open coast. Abundances in the bay were higher than the average abundance along much of the Peruvian coast, but comparable to localized peak values there (Ayón, 2001a; Girón 2001). The higher abundance of larval *E. ringens* in Independencia Bay compared with the open coast suggests that the bay may serve as a nursery area for this species, and may also serve as a refugium for *E. ringens* during El Niño events.

4.1.3 Environmental variables

The MANOVA results for the comparison of environmental variables showed significant main effects for month, station and depth (Table 5, Publication I). Only the surface and 10 m level, in which the fish larvae were collected, were included in the analysis. Clear indications for significant interaction terms could not be found, instead, the three test statistics produced an indifferent picture with always at least one statistic not being significant. For this reason,

interaction terms were not incorporated in the subsequent analysis. Pairwise comparisons (with Bonferroni correction) of the environmental data vector over stations and months were calculated as multivariate contrasts and are summarized in Tables 6 and 7 (Publication I). In the tables, months and stations with the same letter constitute groups of environmental variables which are not significantly different from one another. Table 8 (Publication I) summarizes the principal components of the environmental data. The structure of the principal components showed that temperature was the hydrographically dominant component (explaining 44.8% of the variation), followed by salinity (29.6%); together these two components explained 74.4% of the variability in the oceanographic data. The other two parameters (oxygen and pH) were relatively unimportant.

4.1.4 Relationships between environmental variables and larval fish assemblage

The relation between environmental variables and the larval fish assemblage, analysed by a multivariate logistic model (backward selection), showed that all four environmental parameters had significant effects on species assemblage and that also all two-fold interactions with the exception of temperature * oxygen were significant (Table 9, Publication I).

Table 9 (Publication I) shows a clear statistical relation between environmental parameters and the larval assemblage. Several significant interaction terms show that this relation was of a complex nature. Further conclusions are hard to make, as the environmental quantities did not emerge from a designed laboratory experiment, but were measured in the field, leading to highly correlated values, as could already be seen from the PCA, in Table 8, Publication I. For this reason, no attempt is made to attribute changes of the larval assemblage to one or more particular environmental parameters.

In many bays and estuaries, small-scale fronts commonly form and disperse with each consecutive flood and ebb tide (Vargas et al., 2003), and may affect larval transport from spawning grounds to coastal nurseries (Govoni et al., 1989). The effect of tidal phase on circulation also has been reported to have a major influence on ichthyoplankton distributions in some bays and estuaries (Vargas et al., 2003). My study provides little evidence for the importance of such factors in Independencia Bay, although the scale of the study was rather smaller than some others. There was no clear, general relationship between tidal phase and larval distribution, although the densities of some taxa (*P. jugularis* at Tunga, *Scartichthys* sp. at Panteón (only at night), and *E. ringens* at both stations) were often higher during rising tide and lower near ebb.

4.2 Vertical distribution of fish larvae

Larvae in Independencia Bay showed a well defined vertical distribution, and hence appear capable of maintaining vertical position in spite of the vertical mixing that the absence of a strong thermocline suggests. In general, the 10 m abundances of both individuals and taxa were higher than at the surface. The greatest abundances of *Odontesthes regia regia* were mostly caught at the surface, and a pronounced seasonal variability was observed (Fig. 3, Publication I).

Five major depth groups were determined by cluster analysis (Fig. 8a) at the 20% similarity level in the vertical distribution analysis of samples taken during the day at two depths for all four stations (Publication I). Groups I and II consisted exclusively of surface samples, dominated by *Odontesthes regia regia*. Group III consisted only of one summer sample at Santa Rosa. Group IV was composed predominantly (84.6%) of samples collected at 10 m depth, in which *Normanichthys crockeri*, *Engraulis ringens* and *Scartichthys* sp. dominated. Group V consisted exclusively of samples at 10 m depth (78%). The MDS plot (Fig.8b) also demonstrated a difference in the surface and 10 m depth sample assemblages. Depth stratification of assemblages was evident throughout the bay, even though the shallow water column was well mixed. Classification analyses revealed that depth was more important than map location in distinguishing assemblages; and that the atherinopsid *Odontesthes regia regia* was the only one of the nine most abundant taxa that was consistently most abundant at the surface at all locations. Such a neustonic larval distribution is known in general for atherinopsid larvae (Leis, 1991; Schmitt and Leis, 2000).

Larvae of the Blenniidae (*Scartichthys* sp.), Engraulidae (*Engraulis ringens*), Gerreidae (*Eugerres periche*), Gobiesocidae (*Gobiesox marmoratus* and *Tomicodon petersi*), Normanichthyidae (*Normanichthys crockeri*), Paralichthydae (*Paralichthys microps*), Pinguipedidae (*Prolatilus jugularis*), Kyphosidae (*Doydixodon* sp.), Labrisomidae (*Labrisomus philippi*), and Haemulidae (*Anisotremus* sp.) were sampled at the surface at least once in different months, usually at night (Table 1, Publication I), but were never more numerous there than at 10 m depth (Vélez et al., 2004b).

In a vertical distribution analysis of two depths over 24 hours at two stations (Publication II), the number of taxa at the surface was identical at both stations, but it was higher at 10 m depth at Tunga than at Panteón (Table 3). Two patterns of vertical larval distribution were observed. Most larvae were located mainly at 10 m depth, whereas larvae of *Odontesthes regia regia* occurred mainly at the surface. At Panteón, the number of taxa at both depths tended to be higher at night. Tunga showed nothing but a slight tendency to higher nighttime

taxa numbers at 10 m. There is little evidence for vertical migration except in *O. regia regia*, which may have been more concentrated at the surface during the daytime; and in *G. marmoratus* and *Labrisomus* sp., both of which may avoid the surface during the day and hence might migrate within the lower water column.

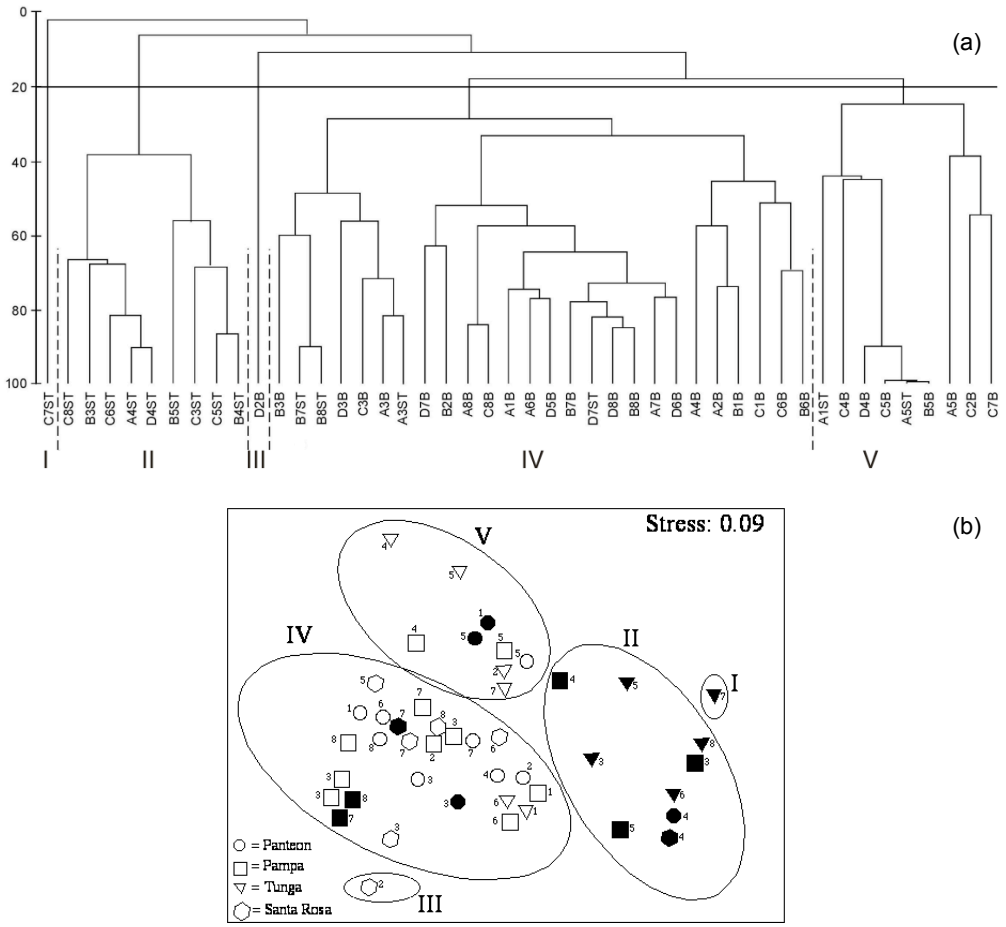

Fig. 8. Vertical classification of the ichthyoplankton sampled in Independencia Bay in the year 2000. Data are log (x+1) transformed. Only the dominant taxa were included in this analysis. (a) Dendrogram of similarities (Bray-Curtis index). A=Panteón, B=Pampa, C=Tunga, D=Santa Rosa, ST=Surface Net, B=Bongo Net. (b) MDS ordinations. Closed symbols=surface samples, open symbols= 10 m samples. Numbers in both plots refer to the month of sampling: 1=January, 2=February, 3=March-April, 4=May, 5=August, 6=September, 7=October, 8=November.

4.3 Seasonal assemblages of fish larvae

The cluster analysis distinguished four seasonal groups at a 20% similarity level, corresponding to larval fish assemblages (Fig. 9a). Group I is composed of summer samples, Group II is composed of March-April samples, Group III includes the surface samples collected predominantly (86%) in autumn and winter, with just over half the samples (57%) taken in autumn. Group IV contains predominantly spring through autumn samples (93%).

The ordination plot (Fig. 9b) clearly shows the small summer and winter groups (I, II), and the mixture of seasons in the other groups.

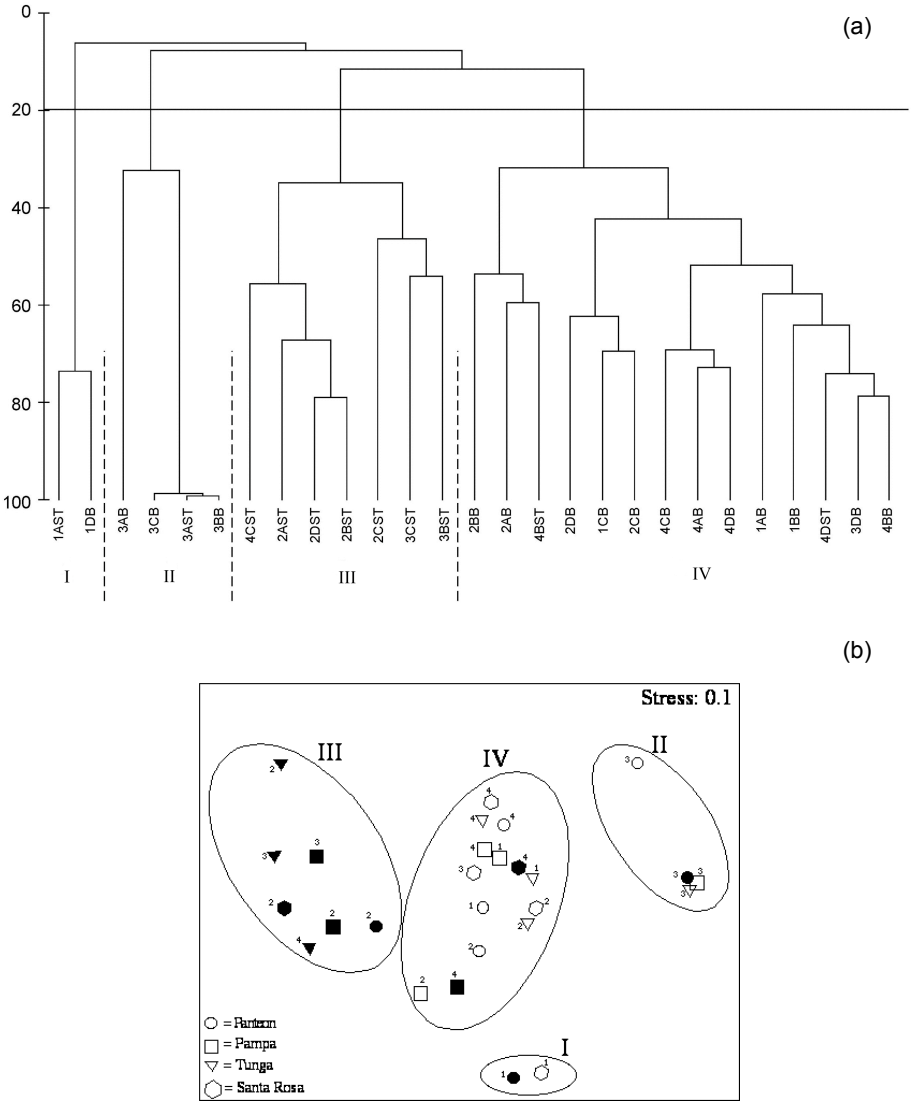

Fig. 9. Seasonal classification of the ichthyoplankton sampled in Indendencia Bay in the year 2000. Data are log (x+1) transformed. Only the dominant taxa were included in this analysis. (a) Dendrogram of similarities (Bray-Curtis index). A=Panteón, B=Pampa, C=Tunga, D=Santa Rosa, ST=Surface Net, B=Bongo Net. (b) MDS ordinations. Closed symbols=surface samples, open symbols= 10 m samples. Numbers in both plots refer to the season of sampling: 1=Summer, 2=Autumn, 3=Winter, 4=Spring.

The results of this study support a hypothesis that various marine organisms synchronize their reproductive seasons in response to local environmental forcing in the bay. Larvae of most species in the bay apparently have a mechanism of staying there (retention), and larvae of coastal pelagic fish (e.g. anchovies, sardines) use the bay as a nursery area. Nearshore species which do not complete their life cycles exclusively in embayments (Group III, Table

10, Publication I) may time their spawning peaks to coincide with reduction in currents, but bay species in Group I and II (Table 10, Publication I) spawn in a pattern that depends less upon seasonal current shifts. Inter-study comparison is not possible because seasonal patterns in primary and secondary productivity in Independencia Bay are poorly documented, and this is the first ichthyoplankton study there. However, it does show that the seasonal spawning patterns of adult fish play a key role in the formation of assemblages of early larvae.

Table 3. Total number of individuals (N), total number of taxa, and densities in n/100 m^3 (D) at the surface and mid-water at the two stations. The totals are also shown.

TIME	SURFACE			MID-WATER			TOTAL		
PANTEÓN	**N**	**Taxa**	**D**	**N**	**Taxa**	**D**	**N**	**D**	**Taxa**
09:00	48	2	60	171	7	96	219	156	7
12:00	2	1	3	223	7	118	225	121	7
15:00	19	3	22	1123	9	483	1142	505	10
18:00	56	3	58	539	10	254	595	312	11
21:00	50	5	51	626	13	272	676	323	13
00:00	9	3	10	703	11	327	712	337	11
03:00	12	2	17	182	10	85	194	102	10
06:00	5	1	7	187	8	76	192	83	8
Total	**201**	**5**	**228**	**3754**	**21**	**1711**	**3955**	**1939**	
TUNGA	**N**	**Taxa**	**D**	**N**	**Taxa**	**D**	**N**	**D**	**Taxa**
09:00	20	1	17	73	14	45	93	62	14
12:00	5	1	4	20	6	10	25	14	6
15:00	4	1	7	76	11	46	80	53	11
18:00	9	2	25	71	12	44	80	69	12
21:00	1	1	7	107	16	73	108	80	16
00:00	1	1	2	48	11	33	49	35	11
03:00	4	2	10	50	9	23	54	33	9
06:00	8	4	7	52	10	33	60	40	12
Total	**52**	**5**	**79**	**497**	**26**	**307**	**549**	**386**	

4.4 Morphological development

4.4.1 *Normanichthys crockeri*

This study describes *Normanichthys crockeri* from recently hatched larvae through transformation from Independencia Bay, Pisco, Peru and supplements the larval description made with *N. crockeri* larvae from Chile by Balbontín and Pérez (1980). Results of the two studies were generally concordant, and no significant differences between Peruvian and Chilean specimens were found. However, we expanded the range of sizes examined compared with the sizes described by Balbontin and Pérez, gave additional information on the sequence of fin formation, fin-ray counts, and fin positions (Table 4, Publication III), and provided new information on skeletal development (Table 2, Publication III).

4.4.1.1 Distinguishing features of *Normanichthys crockeri*

Larval *N. crockeri* are about 1.9 mm at hatching, undergo notochord flexion at approximately 6–9 mm, and transform to the juvenile stage at about 22 mm. The distinguishing characters of the larvae are: an elongate, moderately slender body; a small head with round eyes; preanal length of approximately half of body length; large, pigmented pectoral fins; a distinct dorsal midline melanophore series on the trunk and tail that gradually decreases from as many as 13 more or less evenly spaced melanophores early in the preflexion stage to none by the beginning of the flexion stage; and the presence throughout larval development of pigment ventrally on the gut and tail, at the angular, on the cleithra, and in the caudal region. The pectoral-fin rays begin to develop first, followed by the caudal-fin rays, the second dorsal- and anal-fin rays, the spines of the first dorsal fin, and finally the pelvic-fin rays. There are 36–37 myomeres (Fig. 10).

4.4.1.2 Osteological development of *N. crockeri*

To determine the sequence of ossification of the mandibular arch, suspensorium and opercular series bones, apendicular skeleton, axial skeleton and caudal skeleton, a size series of cleared and stained specimens (Fig. 11) was examined (Tables 2 and 3, Publication III). These aspects of skeletal development in *N. crockeri* are described for the first time in this study. Skeletal development is much like that observed in a variety of scorpaeniform and other fish (e.g., Moser, 1972; Peters, 1983; Potthoff et al., 1984; Yuschak and Lund, 1984; Watson, 1987), and skeletal configuration in the largest cleared and stained specimen was consistent with the description of *N. crockeri* osteology by Yabe and Uyeno, (1996). A perhaps somewhat unusual feature in *N. crockeri* development is the formation of neural arches and vertebral centra before the haemal arches, which differs from the typical scorpaeniform sequence, in which both neural and haemal arches form before the vertebral centra (e.g. Matarese and Marliave, 1982; Washington et al., 1984; Yuschak and Lund, 1984; Matarese and Vinter, 1985), although a *Normanichthys*-like pattern has been reported in Sebastidae (Moser, 1972). A striking feature of skeletal development in *N. crockeri* is the sequence of initial ossification of the opercular series bones, with the preopercle beginning to ossify last, after the interopercle and subopercle. In contrast, the typical scorpaeniform pattern is for the preopercle to begin ossifying before (or in some cases simultaneously with) the subopercular and interopercular bones (e.g., Moser, 1972; Kendall and Vinter, 1984; Yuschak and Lund, 1984). These differences between *Normanichthys* and other scorpaeniforms, with which it commonly has been considered allied, suggest a reexamination of *Normanichthys* phylogenetic relationships may be necessary.

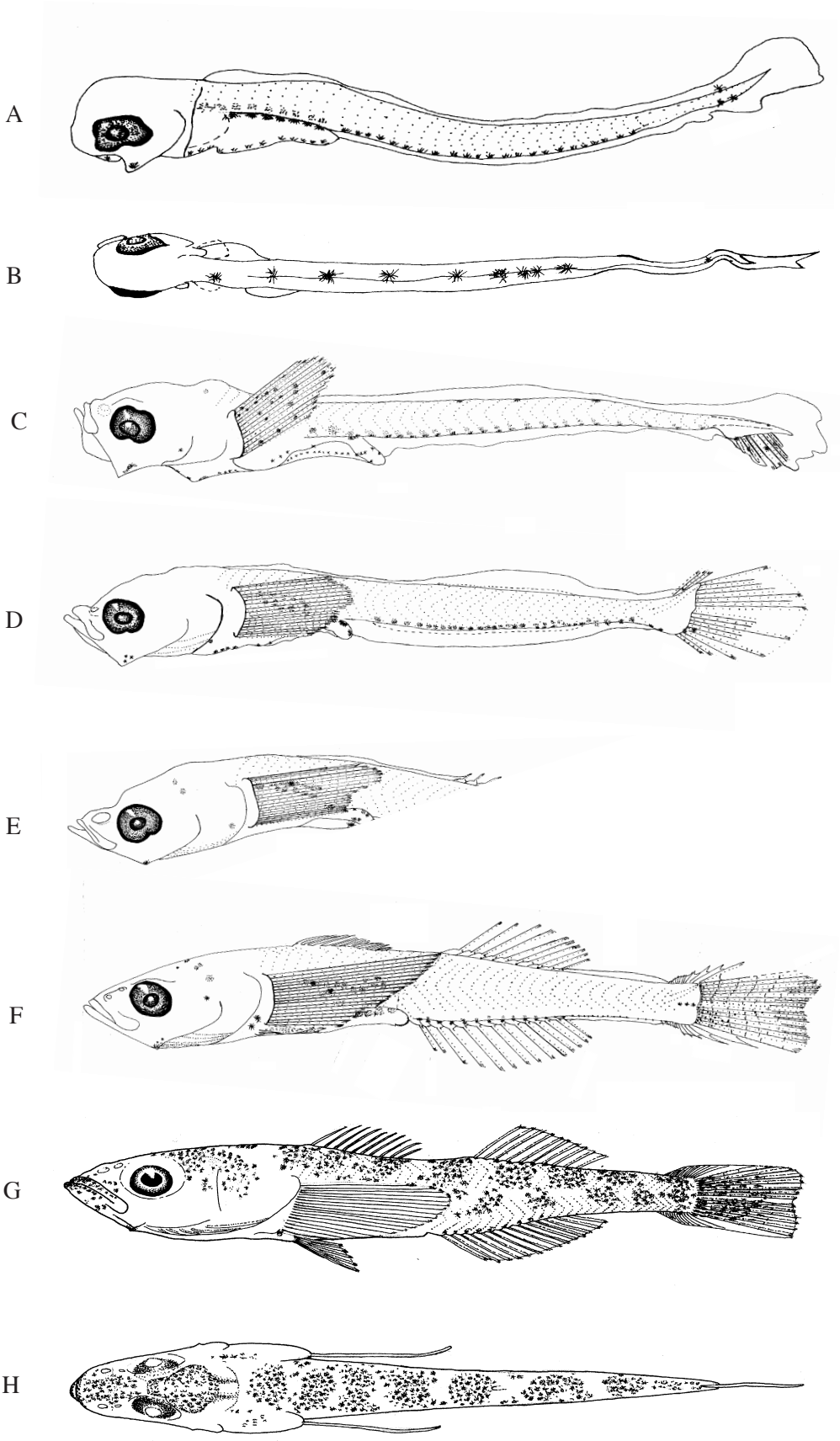

Fig. 10. Larvae of *Normanichthys crockeri*. (A, B)= 2.7 mm (early preflexion, lateral and dorsal view); (C)= 4.9 mm (middle preflexion); (D)= 7.7 mm (flexion); (E)= 9.2 mm (early postflexion); (F)= 16.2 mm (late postflexion); (G, H)= 20.5 mm (transformation, lateral and dorsal view).

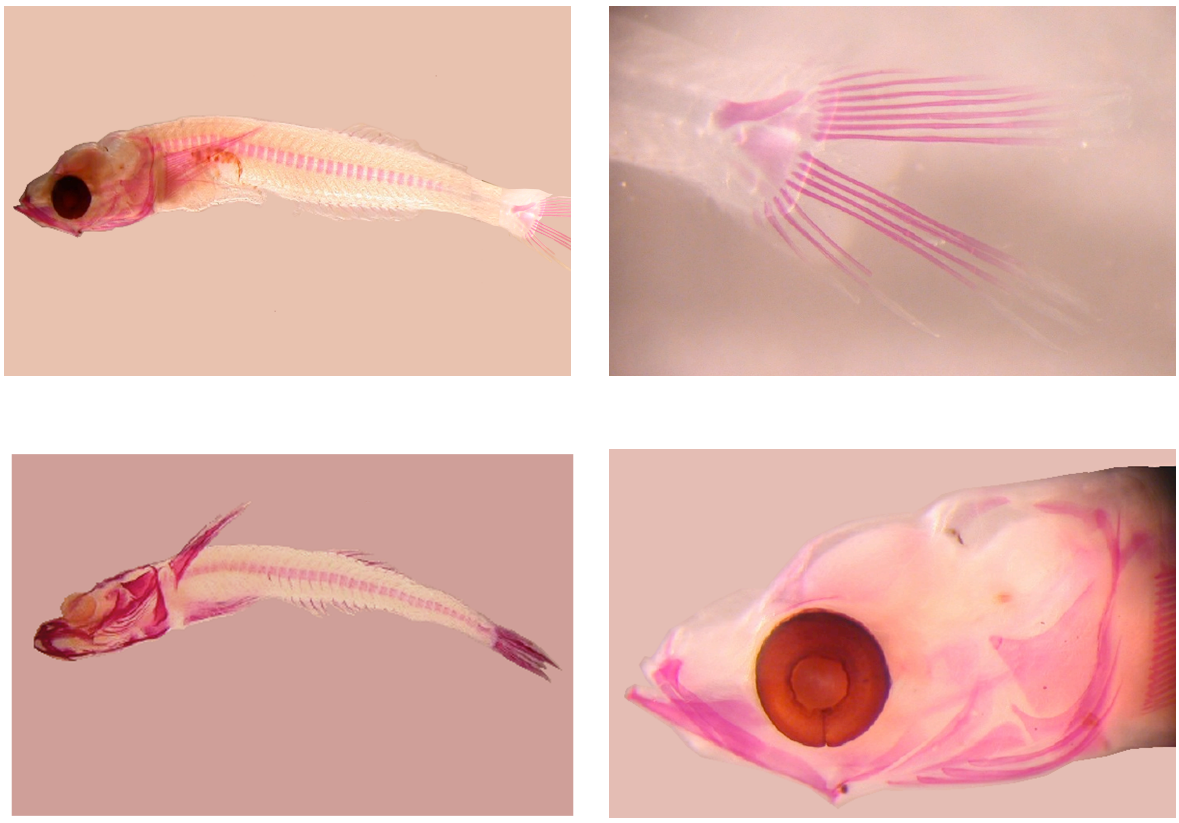

Fig. 11. Cleared and stained larval *Normanichthys crockeri*.

4.4.1.3 Similarities with other larvae

Early larvae of *N. crockeri* resemble those of some cheilodactylids, and to a lesser extent, some aplodactylids and kyphosids. Many kyphosids have similar pigment patterns in the preflexion stage and similar gut length compared with *N. crockeri*, but have far fewer vertebrae (usually 25–27, except *Graus nigra*, a girelline with 34 vertebrae). Larval *G. nigra* are unknown and might resemble *N. crockeri*, but based on other girelline larvae, they may be more heavily pigmented and probably have smaller pectoral fins than *N. crockeri*. Larval Cheilodactylidae and Aplodactylidae have myomere counts (34–36) similar to *N. crockeri*, and some cheilodactylids are pigmented much like *N. crockeri*. However, aplodactylids are more heavily pigmented than *N. crockeri* in the preflexion stage, both aplodactylids and cheilodactylids have pigmented but smaller pectoral fins than *N. crockeri*, and both have a single dorsal fin, in contrast to two separate fins in *N. crockeri.*

4.4.2 *Prolatilus jugularis*

Fischer (1958) described larval *Prolatilus jugularis* from hatching to 4.2 mm. In our study (Vélez et al., 2003b), complete larval development from recently hatched larvae through transformation is described and illustrated for the first time. In Table 3 (Publication IV) we compare some of our results with those of Fischer (1958). Comparable results between the

two studies generally are concordant.

4.4.2.1 Distinguishing features of *Prolatilus jugularis*

Larval *Prolatilus jugularis* hatch at about 2-3 mm, notochord flexion begins at ca. 5.7 mm and ends at ca. 6.9 mm, and transformation begins between 14.2-20.3 mm (probably near 20 mm). The most important diagnostic features of the larvae include a robust body with large head bearing small preopercular spines that begin to form by late preflexion stage; preanal length just under half of body length early in the preflexion stage increasing to near two-thirds of body length early in the postflexion stage; and pigmentation primarily on the snout, opercular region, dorsally on the head and gut, laterally above the hindgut, and on the ventral margin of the tail through early flexion stage. A broad mid-lateral stripe begins to form on the trunk and tail late in the flexion stage and dorsal pigmentation forms on the trunk and tail in the postflexion stage. Pectoral-fin rays begin to form in mid-preflexion stage, followed by principal caudal-fin rays, and then by dorsal-, anal-, and pelvic-fin rays which apparently begin to form simultaneously near the end of preflexion stage. There are 36–37 myomeres (Fig. 12).

4.4.2.2 Similarities with other larvae

The early larvae of *P. jugularis* are morphologically similar to those of a number of species including some scombrids, nemipterids, sparids, microcanthids, blenniids, nomeids and some myctophids. The nemipterids, sparids and microcanthids have fewer myomeres than *P. jugularis* (22-24, 24, and 25 myomeres, respectively, versus 36-37). Most nomeids have 30–31 or ≥40 myomeres; the two eastern Pacific species (both *Psenes*) that have myomere counts similar to *P. jugularis* have preanal length < 50% body length (BL) during the preflexion stage, lack preopercular spines, and have moderately large pelvic fins that form early, far sooner than pelvic fins form in *P. jugularis*. Larvae of the other families commonly have myomere counts in the mid- to high 30s. The blenniids typically have a shorter preanal length than *P. jugularis* (usually ≈ 40% BL except ≈50% in many Salariinae, vs usually ≥50% in *P. jugularis)* and commonly have enlarged and/or pigmented pectoral fins, may develop much larger preopercular spines than *P. jugularis*, and may develop relatively large recurved teeth. Preflexion stage larvae of most scombrid species also usually have preanal length <50% BL (≈50% in *Euthynnus*, >60% in *Acanthocybium*), and all have a larger mouth, larger preopercular spines (except *Scomber*), larger teeth, and develop a longer snout compared with *P. jugularis*. Myctophids generally have an uncoiled, striated gut, most lack preopercular spines, and they commonly are more lightly pigmented than *P. jugularis*.

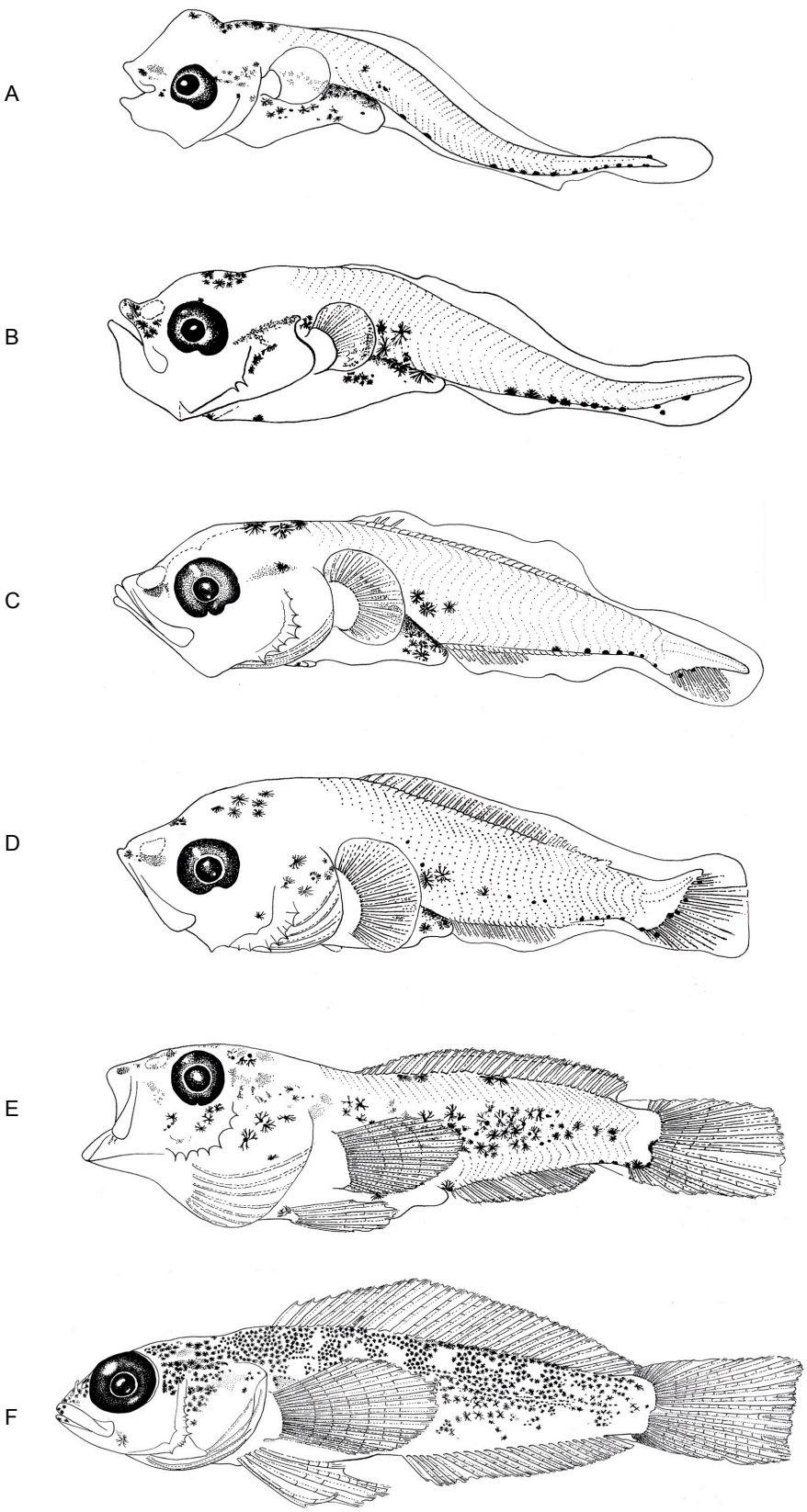

Fig. 12. Larvae of *Prolatilus jugularis*. (A) 2.8 mm (early preflexion); (B) 4.3 mm (mid-preflexion); (C) 6.2 mm (late preflexion; (D) 6.5 mm (mid-flexion); (E) 10.6 mm (late post-flexion); (F) 20.3 mm (transforming). Specimens C and D were slightly less developed than others of similar size.

4.5 Future perspectives

● Future ichthyoplankton studies in the bay should focus on obtaining a better resolution in depth including the near-bottom stratum, and a more extensive sampling spatially and/or temporally to better define recruitment patterns.

● More than one year of sampling should be done in order to assess interannual variability.

● Periodical ichthyoplankton surveys in the Pisco area (with joint physical oceanography and zooplankton surveys) should be effected in an effort to determine the recruitment mechanisms from the Humboldt Current to the coastal zone of Pisco, basically Independencia Bay.

● A combination of rearing studies and developing series of ichthyoplankton samples, as well as more innovative techniques such as biochemical genetics, will be required to fill the gaps in our knowledge on the identification of early developmental stages of marine fishes off Peru.

● Study of ELHS processes from an organismal perspective with the use of elemental analysis is necessary to link fish to habitats and environments over the course of their development based on elemental analyses (e.g. microchemistry: the otoliths of many marine fish show distinct chemical signatures reflecting their movements through the water, offering the potential to trace the pathways of individual larvae as they move from spawning sites to adult settling sites).

● A focus on processes, to determine what factors influence populations, with a long-term goal of developing models to predict future population sizes is needed. To accomplish this, some aspects of the ecology of these animals have to be studied with emphasis on the influence of oceanographic processes on ELHS.

● Investigation of the potential of semi-permanent eddies in the area and associated coastal eddies as retention and transport mechanisms for ELHS would be useful. More interest in ELHS ecology would provide the opportunity to extend an effort further inshore to look specifically at coastal eddy processes and transport pathways from the area.

● Research should focus on the Peruvian ecosystem – Independencia Bay and Pisco Bay –

and the upstream marine ecosystems of the Peruvian coast: a broad look at all ELHS of fishes found in this region has to be taken, with a prime emphasis on the pelagic fish and other commercially important fish larvae found in the area.

5. PUBLICATIONS

This cumulative thesis is composed of four publications as listed below and my contribution to each one is explained.

5.1 Publication I

J. A. Vélez, W. Watson, W. E. Arntz, M. Wolff, S. B. Schnack-Schiel (2004)
Larval fish assemblages in Independencia Bay, Pisco, Peru: Temporal and spatial relationships. Marine Biology (*in press*).

I developed the idea of this paper with my advisors. Plankton sampling and sorting of the samples were done by myself, laboratory work, identifications and processing of data were done in cooperation with the second author. The final version was achieved considering the revisions by all the co-authors.

5.2 Publication II

J. A. Vélez, W. Watson, W. E. Arntz, S. B. Schnack-Schiel (2004)
Vertical distribution and daily migration of ichthyoplankton in Independencia Bay, Pisco, Peru. Journal of Plankton Research, Oxford University Press (*submitted*).

The scientific idea of this paper was developed by myself with the second author. Plankton sampling and sorting of the samples were done by myself. Processing of data was done in cooperation with the second author. The final version was achieved considering the revisions by all the co-authors.

5.3 Publication III

J. A. Vélez, W. Watson, E. M. Sandknop, W. E. Arntz, M. Wolff (2003)*
Larval and osteological development of the Mote Sculpin *(Normanichthys crockeri)* (Pisces: Normanichthyidae) from the Independencia Bay, Pisco, Peru. Journal of Plankton Research, Oxford University Press, Volume **25**, Number 3, Pages 279-290.

I developed the scientific idea of this paper with the second author, I did the sampling and sorted all the ichthyoplankton samples. The larval identification and the laboratory work were made in cooperation with the first two co-authors. The final version was achieved considering the revisions by all the co-authors.

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5.4 Publication IV

J. A. Vélez, W. Watson, E. M. Sandknop, W. E. Arntz (2003)**

Larval development of the Pacific Sandperch (*Prolatilus jugularis*) (Pisces: Pinguipedidae) from the Independencia Bight, Pisco, Peru. Journal of Marine Biological Association of the U.K, **83**, 1137-1142.

Sampling was performed by myself, I developed the scientific idea of this paper with the second author, I sorted all the ichthyoplankton samples. The larval identification and the laboratory work was made in cooperation with the first two co-authors. The final version was achieved considering the revisions by all the co-authors.

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Publication I

Larval Fish Assemblages in Independencia Bay, Pisco, Peru: Temporal and Spatial Relationships.

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Larval Fish Assemblages in Independencia Bay, Pisco, Peru: Temporal and Spatial Relationships

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ABSTRACT: The structure of the larval fish assemblages in Independencia Bay on the coast of Peru was examined using a combination of univariate and multivariate techniques. The plankton of Independencia Bay was sampled during 2000, to ascertain ichthyoplankton composition, abundance, and seasonality. These data were used to assess the function of the bay as spawning and nursery grounds and were related to the regional oceanography. In total, 16,156 fish larvae, representing 34 families, 48 genera, and 48 species were collected. Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae and Atherinidae comprised 96.8% of the larvae captured; the remaining 3.2% included 26 families. Greatest mean larval fish densities, 319–1381/100 m^3, were recorded between September and November, suggesting a major spring spawning period. The most abundant fish larvae during this period were preflexion stage mote sculpins (Normanichthyidae) and newly hatched and preflexion stage anchovies (Engraulidae). A second, smaller summer peak was dominated by preflexion-stage anchovies, followed by preflexion stage mote sculpins. The occurrence of high larval fish densities and the wide range of larval stages suggest that Independencia Bay is a regionally important spawning and nursery ground for marine fish. The Principal Component Analysis showed that temperature and salinity were the dominant variables within the first two principal components, which accounted for 74.4% of the variation in environmental conditions. These conditions varied over time, station and depth, however, interaction terms could not clearly be identified. Fitting a multinomial logistic model showed that larval fish assemblages and environmental conditions were associated in a complex way. The spring and summer ichthyoplankton abundance peaks in Independencia Bay coincided with high zooplankton standing stock and also coincided approximately with the periods of increased upwelling in the area.

Key Words: Ichthyoplankton, Larval fish assemblages, Upwelling area, Peru, Independencia Bay

INTRODUCTION

One of the most productive fishing areas in existence lies off the coast of Peru (Fahrbach et al. 1980). Strong coastal upwelling in this region results from moderately deep (50-100 m) water forced to the surface as a compensation for surface water driven offshore by a combined effect of trade winds, Coriolis force and Ekman transport, bringing nutrient-rich, cool water to the surface (Arntz & Fahrbach 1991). The phytoplankton which thrives within this upwelling zone is fed upon by a variety of creatures including fish larvae. The biomass feeds an important food web culminating in predatory fish, guano birds, and mammals (Mendo, 1997). Coastal regions are important nursery grounds for littoral and shelf fish populations, with shallow areas offering suitable food supply, shelter, and ecophysiological conditions for development of all stages from eggs to juveniles (Blaber & Blaber 1980). It is well documented that many populations of coastal fish depend on such critical areas, at least during part of their life cycle (Weinstein 1979, McHugh 1985).

The knowledge of ichthyoplankton and its ecology is still limited (e. g. Richards 1985); this is especially true for the Pacific coast of South America. Marine fish diversity is high in Peruvian waters, but the larval stages are poorly known (e.g. Vélez et al. 2003). Despite the importance of knowing the processes affecting the dynamics of the coastal ichthyoplankton, most of the ichthyoplankton studies carried out in Peru have focused on mesoscale surveys over the continental shelf and are concentrated on fish with commercial value (Guzmán & Ayón 1995, Guzmán & Carrasco 1996). To date, no scientific information is available on the ecology of ichthyoplankton in Independencia Bay, although it is an area of upwelling and possibly an important spawning and nursery area. It is important to increase our ecological knowledge of Independencia Bay because, as with the entire Pacific basin, it is affected by developments that are tied to major economic activities of fisheries. A study of the distribution patterns of fish larvae contributes to an understanding of the interrelationships among fishes during their early life stages, as well as to an understanding of adult spawning patterns. This paper describes the seasonal abundance of ichthyoplankton in Independencia Bay. The objectives were to: (1) determine the taxonomic composition of fish larvae, (2) assess the seasonal variations of the dominant families. These data are used to assess the inferred function of the bay as a spawning and nursery ground for marine fish in the region.

MATERIALS AND METHODS

Study area

The study was done in Independencia Bay (14º06'-14º20'S; 76º00'-76º18'W), a large, shallow bay situated within the Paracas National Park, Pisco, Peru (Fig. 1). Independencia

Bay is ca. 21 km long and 6.5 km wide, much of the bay is 22-25 meters depth. There are two islands, La Vieja and Santa Rosa. The larger, La Vieja island, is 5.6 km long and 2.4 km wide, and occupies much of the southern half of the mouth of Independencia Bay. It is located in the Humboldt Current marine ecoregion and is a marine upwelling site with elevated levels of primary production all year long, with a higher peak during winter and spring seasons.

Fig. 1. Study area, Independencia Bay, Pisco, Peru. Sampling locations indicated by black points. Black points=main stations (standard sampling); white points=extra stations (additional sampling).

Sample collection

Larvae were collected monthly during January-May, and August-November in 2000. March-April was combined as one sampling period. Plankton was collected with two net types. A 60 cm Bongo with a 0.505 mm mesh net and cod end on one side and a 0.333 mm nitex net and cod end on the other, was towed at a depth of 10 m. A half-meter ring net (0.333 mm nitex mesh) was towed at the surface. Both samplers were equipped with calibrated flowmeters. All tows were taken at a speed of about 1.5 m s^{-1} for 10 min. and samples were preserved in 4% formalin solution immediately after collection. A total of 64 horizontal tows was made during daytime (between 0830 and 1400) at four stations (Santa Rosa, Panteón, Tunga, Pampa) (Fig. 1). An additional 37 daytime tows were made in September. At three stations (Morro Quemado, Pan de Azúcar, Laguna Grande), one sample was taken. At Panteón, two additional samples were taken. At Panteón and Tunga 32 samples were taken, one every three hours, during a 24-hour period. This 24-hour sampling is the subject of a separate paper and it is not included here except for use in compiling the most complete ichthyoplankton species list possible for the bay. The 37 additional samples (Table 1) were included in the composition analysis of the ichthyoplankton, but were not used for distributional analyses.

Using a Niskin bottle, temperature, salinity, pH and dissolved oxygen were measured at four depths (0, 5, 10 and 20 m) during each collection at the four standard stations (Santa Rosa,

Panteón, Tunga, Pampa). The physical data for June, July and December were kindly provided by Dr. J. Tarazona (unpublished data, Universidad Nacional Mayor de San Marcos, Lima, Perú). In the laboratory, zooplankton biomass was measured from each sample using the displacement volume method (Beers 1976), and all fish larvae were sorted from the samples and identified to the lowest taxon possible. Larvae were identified by the series method (Moser 1996, Leis and Carson-Ewart 2000), using a combination of meristic and developmental characters that permitted definitive identification.

Treatment and Data Analysis

Because some specimens could not be identified to genus or species level, abundance data were summed at the family level in the quantitative analyses. The most abundant families in this study were identifiable to species. In each tow, numbers of fish larvae and zooplankton biomass were standardized to the number per 100 m^3 of water filtered. A multivariate ANOVA was used to test for differences in the vector of environmental variables over time, station and depth. Three test statistics were considered for this purpose (Wilk's lambda, Pillai's trace and the Hotelling-Lawley trace), each of which measures specific aspects of the multivariate distances. In order to avoid conclusions on the basis of ambiguous decisions, an effect was considered as present only if all three test statistics produced a significant result. Pairwise comparisons between months, stations and depths were performed by multivariate contrasts with Bonferroni correction. Here, all three previously mentioned statistics coincide, because only two groups are compared. If not stated otherwise, an α error of 0.05 was used in statistical tests.

To determine whether the seasonal abundance changes of larvae of the most common families were statistically significant, Poisson regressions (McCullagh & Nelder 1989) using the number of fish larvae and volume of water filtered per tow were performed on untransformed count data, with months and stations as classification factors. These procedures were run in the GLM (General Linear Model) Module of SAS (SAS 2001). The relations between species assemblage and environmental variables were analyzed by a multinomial logistic model (McCullagh & Nelder 1989), using the LOGISTIC module of SAS (2001). Multivariate analyses, based on the dominant species collected with the Bongo (0.333 mm mesh) and surface nets, were used to examine temporal (seasonal) and spatial (vertical dimension) patterns of the larval fish assemblages. To further examine temporal patterns, and to calculate the similarities between stations and taxa, the Bray-Curtis dissimilarity coefficient was calculated using log (x+1) transformed standardized abundances for each month, station, season, and depth (0 and 10 m) where the samples were taken. The log (x+1) transformation was used to reduce the contribution from numerically dominant

species and to reveal changes among less dominant species (Field et al. 1982). Abundances of taxa were summarized in separate matrices for each factor analyzed; only the eight most abundant taxa were included. A classification (cluster analysis, complete linkage) of the similarity matrices was made for all stations and taxa. Non-metric multidimensional scaling (MDS) was used to graphically display two-dimensional ordination plots of the inter-relationships among samples, based on the relative abundance of each taxon. A low (<0.2) MDS stress coefficient indicates that the multivariate similarity pattern is represented by the plot without much distortion. The PRIMER program was used for these analyses (Clarke & Warwick 1994).

Table 1. Number of tows (Tows), total number of individuals (N), total number of taxa (Taxa), and densities (D= N/100 m^3) at the surface and mid-water across the sampling period (D). Data of the additional sampling during September are listed below the standard sampling data.

	SURFACE				MID-WATER				TOTAL		
STANDARD SAMPLING	**Tows**	**N**	**Taxa**	**D**	**Tows**	**N**	**Taxa**	**D**	**Tows**	**N**	**D**
January	4	11	6	6	4	214	21	97	8	225	103
February	4	1	1	1	4	1200	16	2491	8	1201	2492
March-April	4	29	3	16	4	881	12	484	8	910	500
May	4	26	1	14	4	30	6	14.8	8	56	29
June	-	-	-	-	-	-	-	-	-	-	-
July	-	-	-	-	-	-	-	-	-	-	-
August	4	6	3	3	4	145	14	128,5	8	151	132
September	4	20	1	17	4	557	18	302.1	8	577	319
October	4	104	7	207	4	5935	13	7286.1	8	6039	7493
November	4	13	5	29	4	1764	12	1351.2	8	1777	1380
Total	**32**	**210**	**-**	**-**	**32**	**10726**	**-**	**-**	**64**	**10936**	
ADDITIONAL SAMPLING											
Panteón-24 H	8	201	5	230	8	3754	21	1710	16	3955	1940
Tunga-24H	8	52	5	80	8	497	26	310	16	549	390
Laguna Grande	-	-	-	-	1	3	1	3	1	3	3
Pan de Azúcar	-	-	-	-	1	8	2	6	1	8	6
Morro Quemado	-	-	-	-	1	48	4	61	1	48	61
Panteón	-	-	-	-	2	657	9	294	2	657	294
Total	**16**	**253**	**-**	**-**	**21**	**4967**	**-**	**-**	**37**	**5220**	**-**

RESULTS

Taxonomic composition of the ichthyoplankton

A total of 16,156 fish larvae (Table 1) -representing 34 families, 48 genera, and 48 species- was collected. Twenty-nine families, 35 genera and 36 species were identified (Table 2), 99% of the total larvae were identifiable to at least the level of family. Eight families accounted for 96.8% of total larval abundance: Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae and Atherinidae (Table 2). The remaining 26 families and unidentified taxa contributed 3.2% of the total larvae. Most larvae

not identified to the family level (0.9%) were yolk-sac stage, or damaged larvae. None of the rare taxa contributed more than 0.6% of the total larvae. The three most abundant taxa, the anchovy, *Engraulis ringens*, the mote sculpin, *Normanichthys crockeri* and the blenny, *Scartichthys* sp. together contributed 82.2% of the larvae. These three taxa were found during all months. The next five most abundant families were found during seven months (Gobiesocidae, Labrisomidae and Pinguipedidae), six months (Haemulidae), or five months (Atherinidae). Twenty-eight taxa appeared only in a single month.

Table 2. Total number (N), percent contribution to all fish larvae caught (D= dominance), and frequency (F= % frequency) of capture of the ichthyoplankton taxa collected in Independencia Bay during 2000 (additional sampling is included).

Family	Genus /Species	N	D	F	Family	Genus /Species	N	D	F
Atherinidae	*Odontesthes regia regia*	218	1.3	53.3	**Labrisomidae**	*Labrisomus (philippii?)*	263	1.6	73.3
Blenniidae	*Scartichthys* sp.	2898	18.0	86.7	**Nomeidae**	*Nomeus gronovii*	2	<0.1	13.3
	Hypsoblennius sp.	90	0.6	60.0	**Normanichthyidae**	*Normanichthys crockeri*	5155	31.9	80
Carangidae		3	<0.1	6.7	**Ophidiidae**		5	<0.1	13.3
Centropomidae		1	<0.1	6.7	**Paralichthyidae**	*Paralichthys adspersus*	77	0.5	46.7
Chaenopsidae	*Emblemaria* sp.	2	<0.1	6.7		*P. microps*	12	<0.1	13.3
Cheilodactylidae	*Cheilodactylus variegates*	1	<0.1	6.7		*Etropus ectenes?*	6	<0.1	6.7
Coryphaenidae	*Coryphaena hippurus*	2	<0.1	6.7		*Hippoglossina* sp.	3	<0.1	13.3
Clupeidae	*Sardinops sagax sagax*	7	<0.1	13.3	**Pinguipedidae**	*Prolatilus jugularis*	232	1.4	53.3
Engraulidae	*Engraulis ringens*	5225	32.3	93.3	**Pomacentridae**	*Chromis* sp.	9	<0.1	26.7
Ephippidae	*Parapsettus (panamensis?)*	1	<0.1	6.7		*Abudefduf (?)* sp.	1	<0.1	6.7
Gerreidae	*Eugerres periche*	12	<0.1	13.3	**Sciaenidae**	*Sciaena* sp.	4	<0.1	13.3
Gobiesocidae	*Gobiesox marmoratus*	1346	8.3	73.3	**Scombridae**	*Auxis* sp.	3	<0.1	13.3
	Sicyases sanguineus	22	0.13	6.7	**Scorpaenidae**	*Sebastes capensis*	12	<0.1	13.3
	Tomicodon petersi	2	<0.1	6.7	**Serranidae**		1	<0.1	26.7
Gobiidae	*Evermannia zostetura*	50	0.31	40.0	**Sphyraenidae**	*Sphyraena idiastes*	1	<0.1	6.7
Haemulidae	*Anisotremus* sp.	329	2.0	53.3	**Syngnathidae**	*Leptonotus blainvillianus*	12	<0.1	6.7
Kyphosidae	*Doydixodon* sp.	1	<0.1	6.7	**Unidentified**		146	0.94	26.7
Labridae		2	<0.1	13.3					

Spatial and temporal distribution

Total larval abundance was significantly higher at Santa Rosa than at the other stations, however, there were no statistically significant differences between stations in the total values for any of the dominant families. For surface samples, larval abundance also was highest at Santa Rosa, follow by Panteón, Pampa and Tunga, and the number of taxa was highest at Santa Rosa and Panteón (9), followed by Tunga and Pampa (4) (Table 3). More total individuals, higher standardized total abundance, and more taxa were encountered in the mid-water samples than in the surface samples at all stations, and the highest values at both depths were at Santa Rosa (Table 3). There was a distinct temporal pattern in occurrence in surface and midwater layers (Table 1), the highest value in total larval abundance at both depths occurred in October. A pronounced seasonal variability was observed (Fig. 2), with two peaks in the monthly mean abundance of total fish larvae: one in spring (September-November), dominated by newly hatched mote sculpins and anchovies,

both pelagic shelf species, and a second in summer (January-March), dominated by preflexion-stage anchovies, followed by newly hatched mote sculpin. Greatest mean total abundance during the spring peak was in October (7,493 larvae/100 m^3) suggesting a major spawning period, where Santa Rosa presented the highest abundance. At the summer peak, the greatest mean total abundance was in February (2,492larvae/100 m^3), with highest values at Pampa, Tunga and Panteón. At the summer peak we found 33.3% of the total taxa and at the spring peak, 29.2%. The Figure 3 gives some insight into seasonal variation in abundance of the dominant ichthyoplankton taxa in Independencia Bay. Both abundance peaks are clearly distinguishable.

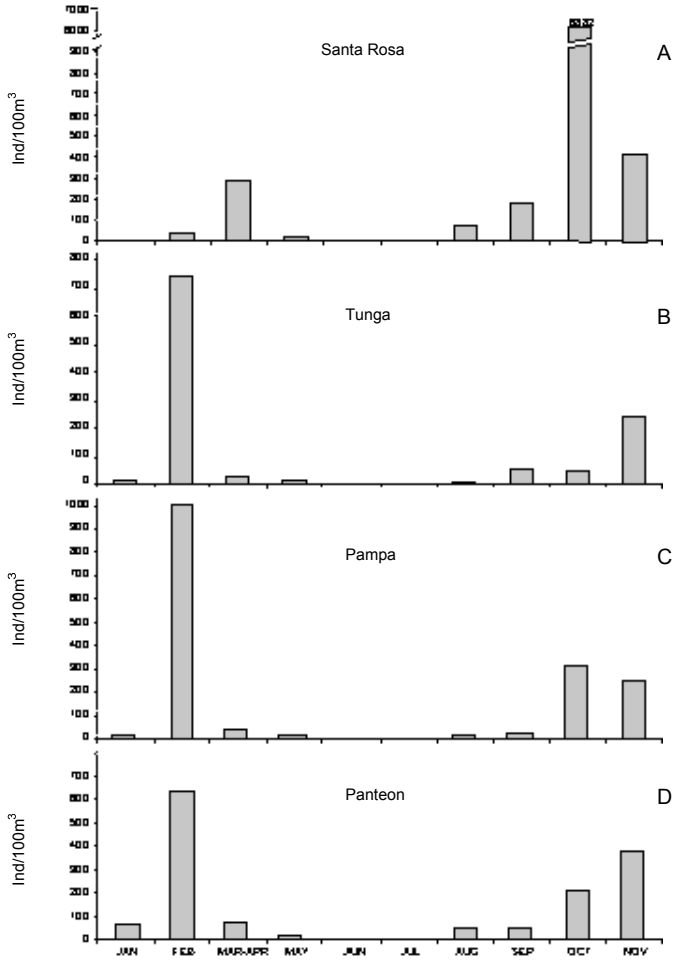

Fig. 2. Mean monthly density (No./100 m^3) of total larvae at the four stations sampled during 2000. Note the different abundance scales for the different stations.

Most individuals of all the most abundant families except Atherinidae were captured in the 10 m (mid-water) stratum (Table 4). The abundances of Engraulidae, Gobiesocidae, Labrisomidae, Normanichthyidae and Pinguipedidae were higher at Santa Rosa than at the other stations, while Atherinidae and Haemulidae were more abundant at Tunga, and the Blenniidae were most abundant at Panteón.

Table 3. Total number of fish larvae (N), total density (D= ind/100 m^3), total number of taxa (Taxa), number of tows (Tows) and temperature ranges (T in °C) at surface and mid-water column pooled across the four stations during the study period (standard sampling only).

Station	Surface					Mid-water					
	N	D	Taxa	Tows	T	N	D	Taxa	Tows	T	Total D
Pampa	25	73	4	8	14.4-20.3	1718	1815	20	8	13.9-15.7	1888
Tunga	33	55	4	8	14.4-19.1	736	1099	19	8	13.5-17.0	1154
Panteón	37	95	9	8	14.0-17.1	1285	1514	20	8	13.7-16.9	1609
Santa Rosa	115	509	9	8	13.7-16.9	6987	7685	23	8	13.4-15.8	8194

Table 4. Total density (larvae/100 m^3), Dominance (D=% contribution to the summed abundance of the dominant taxa), percent in upper and lower regions of the water column, and adult habitats (N=neritic; B=benthic; CP=coastal pelagic) of dominant taxa during 2000 in Independencia Bay (standard sampling only).

Taxa	Total density	D	% upper	% bottom	Adult habitat
Engraulis ringens	48462	40.0	2.8	97.2	CP
Normanichthys crockeri	56947	46.9	2.1	97.9	N
***Scartichthys* sp.**	2749	2.3	0.7	99.3	B
Gobiesox marmoratus	5183	4.3	1.4	98.6	B
***Anisotremus* sp.**	4428	4.5	0.9	99.1	N
***Labrisomus* sp.**	456	0.4	0	100	B
Prolatilus jugularis	1452	1.2	1.0	99.0	B
Odontesthes regia regia	643	0.5	90.6	9.4	N

Seasonal spawning, inferred from larval abundances, could be classified into four general patterns (Fig. 3). These were: winter-spring spawning, as exemplified by *O. regia regia* (Fig. 3H); and spawning throughout much or all of the year, but with a distinct spring maximum, exemplified by *G. marmoratus* (Fig. 3D) and *N. crockeri* (Fig. 3B), with a principal spawning peak in spring and a smaller peak in summer, exemplified by *E. ringens* (Fig. 3A), *P. jugularis* (Fig. 3G). *Labrisomus* sp. (Fig. 3F) and *Scartichthys* sp. (Fig. 3C), and with a principal peak in summer and a smaller peak in spring, exemplified by *Anisotremus* sp. (Fig. 3E).

Odontesthes regia regia was present in five months (Fig. 3H) at all four stations, with peak abundance in September (24 larvae/100 m^3); the high September and November abundances were at Tunga, and the high values during the other months were at the other stations. Larvae appeared only at the surface, except in May and August, when a few also were captured at 10 m depth at Santa Rosa.

Gobiesox marmoratus was present most of the year (Fig. 3D) at all four stations, with peak abundance in October (307 larvae/100 m^3); the peak was apparent at all four stations. Larval abundance at Pampa was slightly higher in summer than during October. *G. marmoratus* was found only at 10 m depth, except in August when some larvae were captured at the surface at Panteón. *Normanichthys crockeri* was found throughout the year (Fig. 3B) at all four stations, with peak larval abundance in October (4,731 larvae/100 m^3); this peak was

primarily at Santa Rosa and Pampa. Abundances during November were highest at Panteón and Tunga. Larvae were present only at 10 m depth except in October when some were captured at the surface at Santa Rosa, and in October and November at Pampa.

Engraulis ringens was present throughout the year (Fig. 3A) at all four stations, with peaks of abundance in October (2,027 larvae/100 m^3) and February (1,953 larvae/100 m^3). The October peak was primarily at Santa Rosa and the February peak was at the other stations. Larvae were collected primarily at 10 m depth; a few were collected at the surface at Santa Rosa and Panteón. *Prolatilus jugularis* occurred during most of the year (Fig. 3G) at all four stations, with peaks in October-November (59.9-72.7 larvae/100 m^3) and February (8.3 larvae/100 m^3). The spring peak was most apparent at Tunga, Panteón and Santa Rosa, and the small summer peak occurred only at Pampa. *P. jugularis* was present mainly at 10 m depth; a few were collected at the surface at Panteón and Tunga. *Labrisomus* sp. occurred throughout most of the year (Fig. 3F) at all four stations, with peak larval abundance in October (32 larvae/100 m^3) and February (3.3 larvae/100 m^3). Only the spring peak was apparent at Panteón and Santa Rosa; the small summer peak occurred at Tunga and Pampa. In September there was another period of relatively high abundance (3.2 larvae/100 m^3) at Tunga. Larvae were collected only at 10 m depth. *Scartichthys* sp. occurred throughout the year (Fig. 3C) at all four stations, with abundance peaks in October (130 larvae/100 m^3) and summer (January, 43 larvae/100 m^3, February, 14.5 larvae/100 m^3). The October peak was primarily at Panteón, Pampa and Santa Rosa, and the summer peak at Tunga. *Scartichthys* sp. was present only at the 10 m depth except in October, when some larvae were captured at the surface at Santa Rosa.

Anisotremus sp. was found most of the year (Fig. 3E) with. *Anisotremus* sp. was present at all four stations, with peak abundance in February (433 larvae/100 m^3) and possibly in October (86.3 larvae/100 m^3). The summer peak was at Tunga and Pampa, and the spring peak at Santa Rosa and Panteón. Larvae were found only at 10 m depth.

Environmental variables

The oceanographic conditions of Independencia Bay are typical of cold coastal waters, due to coastal upwelling. In general, vertical similarities in temperature and salinity reflect the extent of vertical mixing in the Bay (Fig. 4). Because each of the environmental parameters tended to follow a similar seasonal pattern at each of the four depths sampled. We present here only the two depths (0 and 10 m) where the fish larvae were collected. Results of MANOVA, Principal Components (PCA), and Multivariate Multiple Comparisons analyses on the environmental data are summarized in Tables 5-8.

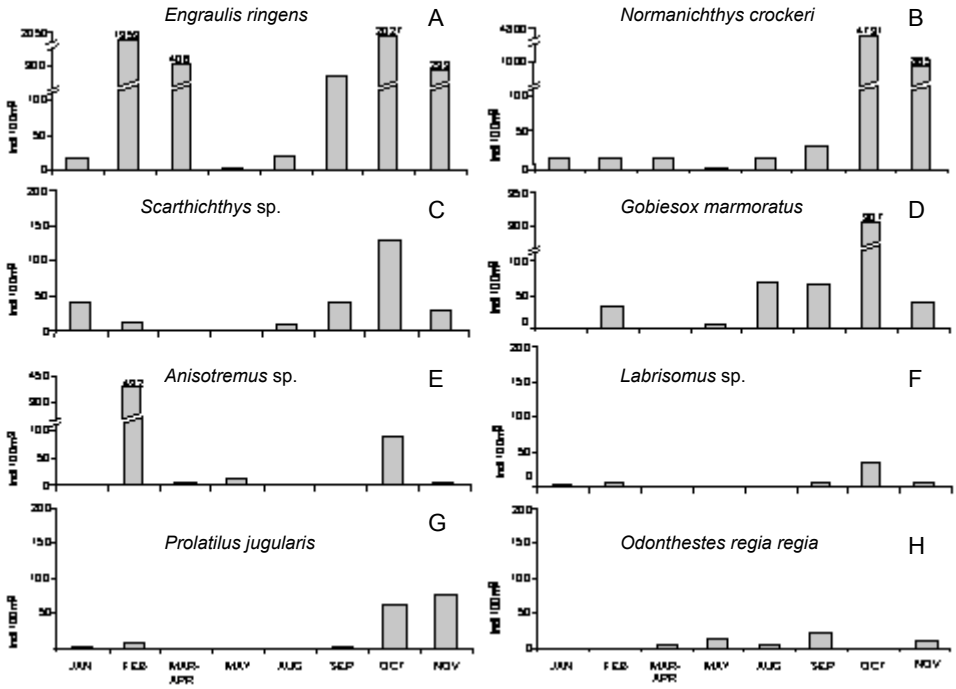

Fig. 3. Mean monthly densities (No./100 m^3) of the most abundant ichthyoplankton taxa collected in Independencia Bay during 2000. Note the differences in scale.

The MANOVA results for the comparison of environmental variables showed significant main effects for month station and depth (Table 5). Only the 0 m and 10 m level, in which the fish larvae were collected, were included in the analysis. Clear indications for significant interaction terms could not be found, instead, the three test statistics produced an indifferent picture with always at least one statistic being not significant. For this reason, interaction terms were not incorporated in the subsequent analysis. Pairwise comparisons (with Bonferroni correction) of the environmental data vector over stations and months were calculated as multivariate contrasts and are summarized in Tables 6 and 7. In the tables, months and stations with the same letter constitute groups of environmental variables which are not significantly different from one another. Table 8 summarizes the principal components of the environmental data. The structure of the principal components showed that temperature was the hydrographically dominant component (explaining 44.8% of the variation), followed by salinity (29.6%); together these two components explained 74.4% of the variability in the oceanographic data. The other two parameters (oxygen and pH) were relatively unimportant.

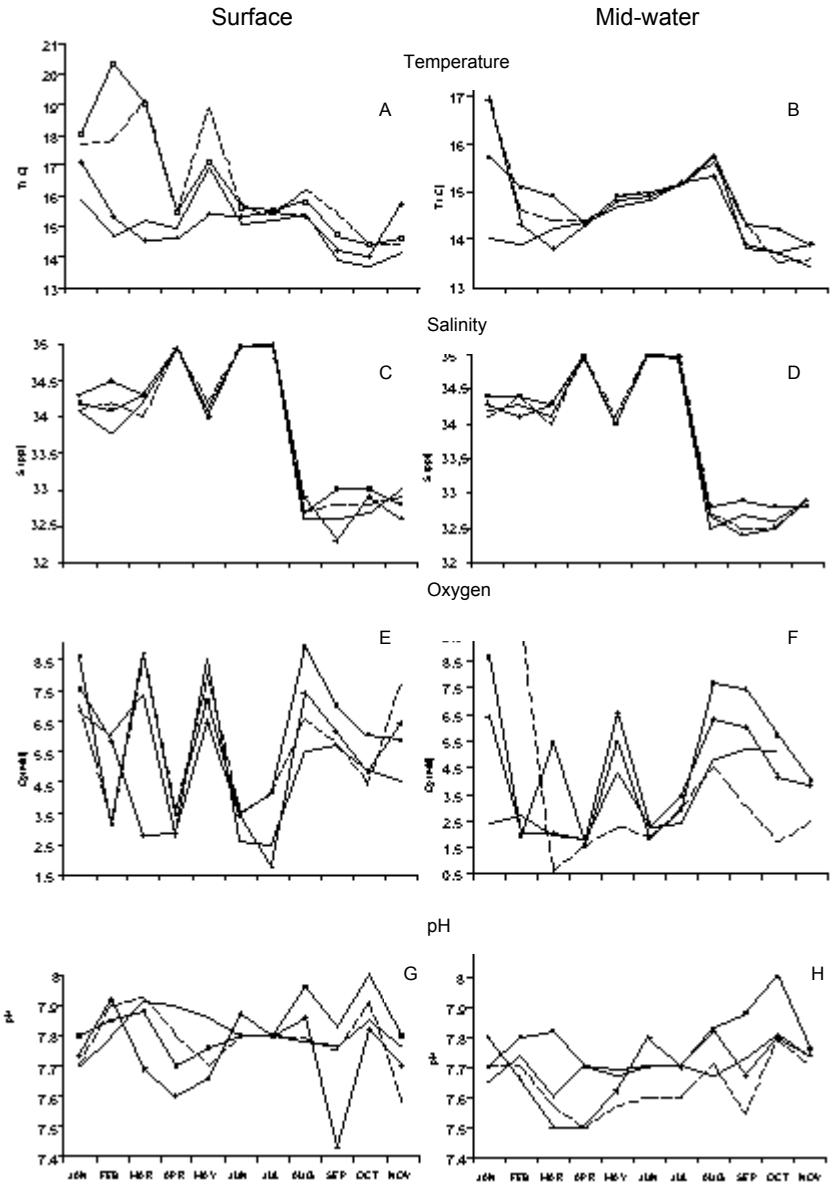

Fig. 4. Spatial and temporal variations in mean temperature (A, B), salinity (C,D), oxygen (E,F) and pH (G,H) at the surface and 10 m depth for each station in Independencia Bay during 2000. Solid line=Santa Rosa, dashed line=Tunga, solid line with circles=Pampa, solid line with cross=Panteón.

Table 5. Summary of the MANOVA results for the environmental data. Temperature, Salinity, O_2 and pH jointly constituted the dependent vector. Num DF=degrees of freedom for the numerator of the F statistic; Den DF= degrees of freedom for the denominator of the F statistic.

Source of Variation	Type of Test											
	Wilk's Lambda				Pillai's Trace				Hotelling-Lawley Trace			
(Main Effects)	P	F	Num DF	Den DF	P	F	Num DF	Den DF	P	F	Num DF	Den DF
Month	<0.0001	15.48	28	66.32	<0.0001	4.31	28	84	<0.0001	112.83	28	36.16
Station	0.0004	3.8	12	47.91	0.0014	3.21	12	60	0.0008	4.27	12	27.46
Depth	<0.0001	15.0	4	18	<0.0001	15.0	4	18	<0.0001	15.0	4	18
(Interaction Terms)												
Month x Station	0.0494	1.46	84	73.55	0.0459	1.45	84	84	0.0841	1.46	84	44.77
Month x Depth	0.0502	1.65	28	66.32	0.0800	1.50	28	84	0.0438	1.83	28	36.16
Station X Depth	0.0481	1.98	12	47.91	0.0421	1.98	12	60	0.0711	1.96	12	27.46

Table 6. Mean values and pairwise multivariate comparisons with Bonferroni correction of the environmental data vector (T=Temperature, S=Salinity, O_2=Oxygen and pH) over months. N=Number of observations. Means with the same letter (Grouping column) are not significantly different.

300 NET		MEAN VALUES				
Month	**N**	**T (°C)**	**S (ppt)**	**O_2(ml/l)**	**pH**	**Grouping**
Jan	4	15.90	34.25	6.80	7.71	A
Feb	4	14.48	34.30	4.10	7.73	A
Mar-Apr	4	14.33	34.18	2.48	7.62	A
May	4	14.83	34.03	4.62	7.64	A
Aug	4	15.60	32.68	5.81	7.76	B
Sep	4	14.08	32.63	5.41	7.71	B C D
Oct	4	13.78	32.60	4.15	7.85	C
Nov	4	13.70	32.88	3.69	7.65	D
STANDARD NET		***MEAN VALUES***				
Month	**N**	**T (°C)**	**S (ppt)**	**O_2(ml/l)**	**pH**	**Grouping**
Jan	4	17.15	34.18	7.49	7.73	A
Feb	4	17.03	34.15	4.51	7.87	A
Mar-Apr	4	16.95	34.20	6.86	7.85	A
May	4	17.08	34.08	7.51	7.75	A
Aug	4	15.68	32.73	7.10	7.85	B
Sep	4	14.55	32.68	6.16	7.70	B
Oct	4	14.13	32.85	5.05	7.90	B
Nov	4	14.70	32.83	6.13	7.71	B

Table 7. Multiple Comparisons Analyses (Scheffe's test) on the environmental data. Mean values for the stations are listed. Mean with the same letter (S.G. column) are not significantly different. N=Number of observations, T=Temperature; S.G=Scheffe Grouping; S=Salinity, O_2=Oxygen.

300 NET		MEAN VALUES				
Station	**N**	**T (°C)**	**S (ppt)**	**O_2(ml/l)**	**pH**	**Grouping**
Pampa	8	14.84	33.55	5.76	7.81	A
Panteón	8	14.58	33.40	4.65	7.70	A
Santa Rosa	8	14.19	33.41	3.87	7.66	A
Tunga	8	14.74	33.40	4.24	7.66	A
STANDARD NET		**MEAN VALUES**				
Month	**N**	**T (°C)**	**S (ppt)**	**O_2(ml/l)**	**pH**	**Grouping**
Pampa	8	16.74	33.51	6.92	7.86	A
Panteón	8	15.19	33.48	5.92	7.73	A
Santa Rosa	8	14.96	33.39	6.18	7.80	A
Tunga	8	16.74	33.46	6.38	7.78	A

Table 8: Principal components (loadings) of the environmental data. T=temperature; S=salinity, O_2=oxygen; pH=potential of hydrogen, PC=principal component.

	PC 1	PC 2	PC 3	PC 4
T (°C)	0.6376	0.2361	-0.0451	-0.7318
S (ppt)	0.2821	0.7758	0.3006	0.4775
O_2 (ml/l)	0.5743	-0.2472	-0.6307	0.4595
pH	0.4288	-0.5302	0.7139	0.1585

Relationships between environmental variables and larval fish assemblage

The relation between environmental variables and the larval fish assemblage, analysed by a multivariate logistic model (backward selection) , showed that all four environmental

parameters had significant effects on species assemblage and that also all two-fold interactions with the exception of temperature x oxygen were significant (Table 9).

Table 9 shows that there clearly is a statistical relation between environmental parameters and the larval assemblage. The many significant interaction terms show that this relation is of complex nature. Further conclusions are hard to make, as the environmental quantities did not emerge from a designed laboratory experiment, but were measured in the field, leading to highly correlated values, as could already be seen from the PCA in Table 8. For this reason, no attempt is made to attribute changes of the larval assemblage to one or more particular environmental parameters.

Table 9. Results of fitting a multinomial logistic model to species assemblage. Only the main families were included. DF=Degrees of freedom, SE=Standard Error.

Parameter	DF	Estimate	SE	Wald Chi-Square	P
Intercept Atherinidae	1	-1982.2	348.9	32.2743	<0.0001
Intercept Blenniidae	1	-1980.4	348.9	32.2164	<0.0001
Intercept Engraulidae	1	-1976.7	348.9	32.0982	<0.0001
Intercept Gobiesocidae	1	-1976.5	348.9	32.0900	<0.0001
Intercept Haemulidae	1	-1976.4	348.9	32.0888	<0.0001
Intercept Labrisomidae	1	-1976.4	348.9	32.0882	<0.0001
Intercept Normanichthyidae	1	-1972.1	348.9	31.9492	<0.0001
Intercept Paralichthyidae	1	-1971.6	348.9	31.9310	<0.0001
Temperature	1	3.6487	6.4344	0.3216	0.5707
Salinity	1	50.2196	11.7772	18.1828	<0.0001
Oxygen	1	26.2364	3.7506	48.9330	<0.0001
pH	1	275.4	46.1096	35.6667	<0.0001
Temperature X Salinity	1	0.4619	0.1025	20.3065	<0.0001
Temperature X pH	1	-2.2206	0.8366	7.0454	0.0079
Salinity X Oxygen	1	-0.2252	0.0331	46.3835	<0.0001
Salinity X pH	1	-7.1925	1.5428	21.7337	<0.0001
Oxygen X pH	1	-2.4054	0.4621	27.0912	<0.0001

Vertical assemblages

Five major depth groups were determined by cluster analysis (Fig. 5a) at the 20% similarity level. Group I and II consisted exclusively of surface samples, where *Odontesthes regia regia* was most abundant and overwhelmingly dominant. Group III consisted only of one sample in summer at Santa Rosa. Group IV was composed predominantly (84.6%) of samples collected at 10 m depth, where *Normanichthys crockeri* , *Engraulis ringens* and *Scartichthys* sp. were dominant. Group V consisted mainly of mid-water samples (78%). The MDS (Fig. 5b) plot also showed that the assemblage at the surface and 10 m differed. Depth stratification of assemblages was evident although the water column was well mixed in this shallow bay.

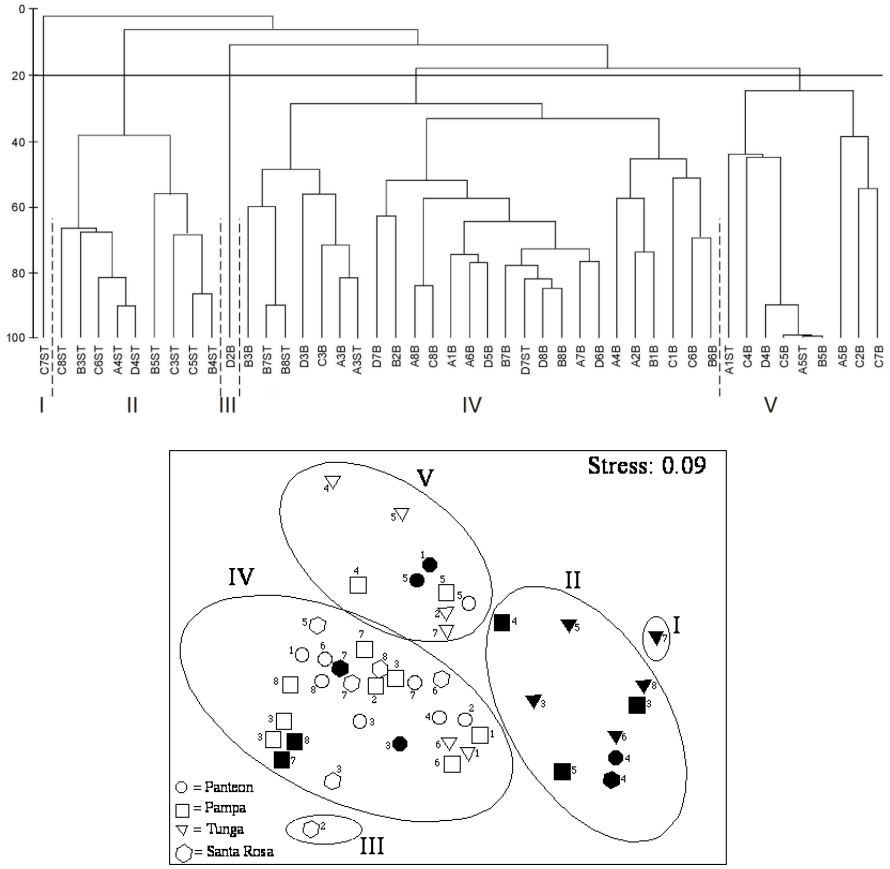

Fig. 5. Vertical classification of the ichthyoplankton sampled in Independencia Bay in 2000. Data are log (x+1) transformed. Only the dominant taxa were included in this analysis. (a) Dendrogram of similarities (Bray-Curtis index). A=Panteón, B=Pampa, C=Tunga, D=Santa Rosa, ST=Surface Net, B=Bongo Net. (b) MDS ordinations. Closed symbols=surface samples, open symbols= 10 m samples. Numbers in both plots refer to the month of sampling: 1=January, 2=February, 3=March-April, 4=May, 5=August, 6=September, 7=October, 8=November.

Seasonal assemblages

The cluster analysis distinguished four seasonal groups at a 20% similarity level, corresponding to larval fish assemblages (Fig. 6a). Group I is composed of summer samples, Group II is composed of March-April samples, Group III is composed of surface samples collected predominantly (86%) in autumn and winter, with just over half the samples (57%) taken in autumn, and group IV contains predominantly spring through autumn samples (93%). The ordination plot (Fig. 6b) clearly shows the small summer and winter groups (I, II), and the mixture of seasons in the other groups.

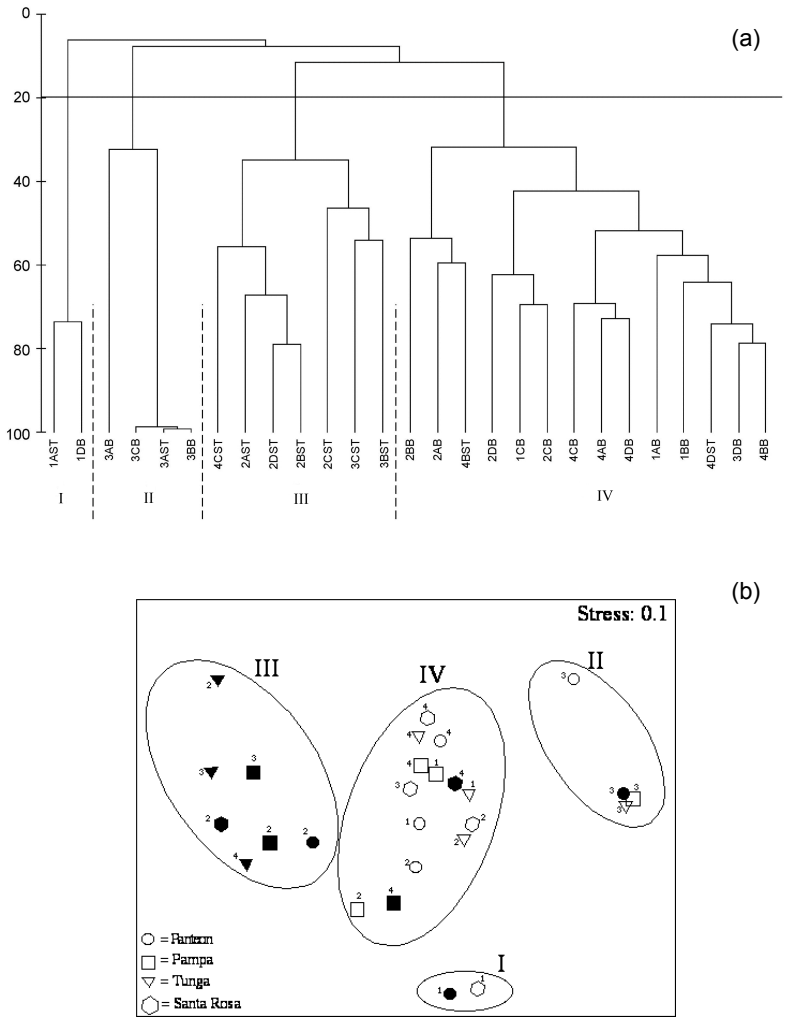

Fig. 6. Seasonal classification of the ichthyoplankton sampled in Indendencia Bay in 2000. Data are log (x+1) transformed. Only the dominant taxa were included in this analysis. (a) Dendrogram of similarities (Bray-Curtis index). A=Panteón, B=Pampa, C=Tunga, D=Santa Rosa, ST=Surface Net, B=Bongo Net. (b) MDS ordinations. Closed symbols=surface samples, open symbols= 10 m samples. Numbers in both plots refer to the season of sampling: 1=Summer, 2=Autumn, 3=Winter, 4=Spring.

DISCUSSION AND CONCLUSIONS

Independencia Bay is a productive marine ecosystem that contains cold, low salinity waters derived from the adjacent Humboldt Current. Independencia Bay also is subject to physical variability, influenced by strong currents. Perhaps owing to its variability, and probably owing also to the high production, the bay supports an abundant and varied ichthyoplankton. However, only a small proportion of the total taxa (16.7%: 8 species) contributed most of the total abundance of fish larvae (96.8%). The numerically dominant taxa were Engraulidae, Normanichthyidae, Blenniidae, Gobiesoscidae, Haemulidae, Labrisomidae, Pinguipedidae and Atherinidae. All of these except Engraulidae are resident taxa that most likely complete their life cycles within the bay.

Composition of the larval fish assemblage

The composition of larval fish assemblages in coastal waters is generally related to the local current regimes, habitat types and water masses occurring in the region. All of the families listed in table 10 have species that are most abundant in bays but also may occur to some extent near shore along the open coast, as well as species that are most abundant inshore along the open coast but also occur in bays (Mongard 1981, Leis 1994, Hildebrand 1996, Beltran-Leon & Rios 2000). The dominant species in these families that we found during our study are primarily those associated with bays, based on these earlier studies. Fish larvae from this study could be divided into four groups on the basis of their adult habitat (Table 10): (I) inshore, benthic species; (II) inshore, neritic species; (III) coastal pelagic species that do not complete their life cycle exclusively in the bay; (IV) epi-and mesopelagic oceanic species. Most of the members of groups I and II are very common in Independencia Bay as adults (Reynaga and Mendo 2002) and, as evidenced by collections of eggs, preflexion and flexion stages, we suspect that they spawn and complete their life cycles within the bay. The larvae of these two groups constituted > 66.6% of all larvae collected at all stations. Group III constituted 32.5% of the total larvae collected, of which 99.4% was constituted by *Engraulis ringens*. Group IV, the oceanic taxa, contributed less than 1% of the total larvae in the bay. Apparently the bay is not an important nursery area for the oceanic species, but it supports a suite of inshore species and is likely to be a critical habitat for them.

Table 10. Families of fish larvae grouped on the basis of their adult habitats reported in the literature (Nelson, 1994).

Group I		**Group II**	**Group III**	**Group IV**
(Inshore-Benthic species)		**(Inshore-Neritic species)**	**(Coastal Pelagic fish, not bay dependent)**	**(epi- and mesopelagic species)**
Blenniidae	Labrisomidae	Atherinidae	Engraulidae	Nomeidae
Chaenopsidae	Ophidiidae	Centropomidae	Clupeidae	Scombridae
Cheilodactylidae	Paralichthyidae	Haemulidae	Coryphaenidae	
Ephippidae	Pinguipedidae	Labridae	Kyphosidae	
Gerreidae	Scorpaenidae	Normanichthyidae	Sphyraenidae	
Gobiesocidae	Serranidae	Pomacentridae	Carangidae	
Gobiidae	Syngnathidae	Sciaenidae		

Spatial and Temporal Distribution

The young age of most larvae collected in this study (mostly preflexion stage) suggests that the temporal and spatial patterns mainly reflect spawning seasons and localities (i.e., inside or outside the bay) of adults. Most of the abundant taxa except engraulids probably spawn primarily or entirely inside the bay; *E. ringens* spawns mainly along the open coast (Ayón 2001a, 2001b, Girón 2001). In the Pisco area larval abundance of *E. ringens* is high in the coastal zone to 46.3 km from shore (Ayón 2001b), but it clearly spawns in Independencia Bay, too. In the bay, where fish larvae are predominantly species that most likely complete their life cycles inside the bay (groups I and II, Table 10), the larvae probably are retained by

the circulation pattern within the bay and possibly by larval behaviour. Yamashiro et al. (1990), Moron and Campos (1998) and Moron (pers. Comm.) demonstrated the presence of anticyclonic circulation in the central bay. The central bay (north of La Vieja Island) is relatively rich in plankton and consistently holds high abundances of fish eggs and larvae. Larvae of all sizes were retained in the anticyclonic eddy. Although no larval length or current measurements were made in this study, a qualitative examination of the samples suggested that larvae tended to be larger at Santa Rosa than at the other stations. The apparent larger larval sizes at Santa Rosa may reflect an inability of the smaller larvae to maintain position in the stronger currents at this station which is closer to the open ocean. Alternatively it might reflect preferential movement of the older larvae into the area, possibly because of higher food availability (zooplankton volumes were always higher at Santa Rosa than at the other stations), or for settlement. Hydrographic conditions that retain planktonic eggs and larvae within bays (Doyle et al. 1993), together with enhanced densities of food, may allow developing larvae to grow rapidly, thus helping them to avoid predators and resist being dispersed by currents (Bourne & Govani 1988, Olney & Boehlert 1988). The species composition differed between summer and spring, but the dominant species were found in both seasons, except *Odontesthes regia regia*, which was absent in both February and October, but present in November. The reason for this different seasonal spawning pattern is unclear, because we do not see any difference between the stations during the peak. Since *Odontesthes regia regia* larvae are neustonic, wind-driven surface transport may be important and the wind pattern would favor larval retention in the bay. Another possibility to consider is that there may be some adult spawning habitat requirement that is available only during part of the year and that drives the pattern. The spring and summer ichthyoplankton abundance peaks in Independencia Bay coincided with high zooplankton standing stock and also coincided approximately with the periods of increased upwelling in the area (Fig. 7). Presumably, spawning in the bay during summer and early spring in association with strong upwelling periods permits larvae to take advantage of the increased planktonic production. The May sample had the lowest monthly mean larval density (29.2 larvae/100 m^3). Cabello et al. (2002) detected in mid-May to mid-June 2000 high concentrations of oil and grease coming from fishery effluents and discussed the presence of a red tide associated with an increase in total suspended solids, pH and dissolved oxygen at Paracas Bay (north of Independencia Bay). The red tide was also observed during the May ichthyoplankton sampling in Independencia Bay and it is possible that the low larval abundance in that month could be related to these phenomena. Comparing the abundances of *E. ringens*, the most important Peruvian fisheries resource, with results from IMARPE studies during 2000 in other areas along the Peruvian coast, shows that larval abundances generally were of the same order of magnitude both in the bay and off the open coast. Abundance was higher in the bay

than along much of the coast and was comparable to that in localized high abundance areas along the Peruvian coast (Ayón 2001a, Girón 2001). Higher abundance of larval *E. ringens* in Independencia Bay compared with waters along much of the open coast suggests that the bay may, to some extent, serve as a nursery area for this species. In addition, it is possible that the bay could serve as a refugium during El Niño events for species such as *E. ringens*. In the California Current region plankton production near shore remains relatively high during El Niño events compared with more seaward waters, thus providing food and increasing larval survival of species such as *Sardinops sagax* in the near-shore zone compared with the oceanic regions.

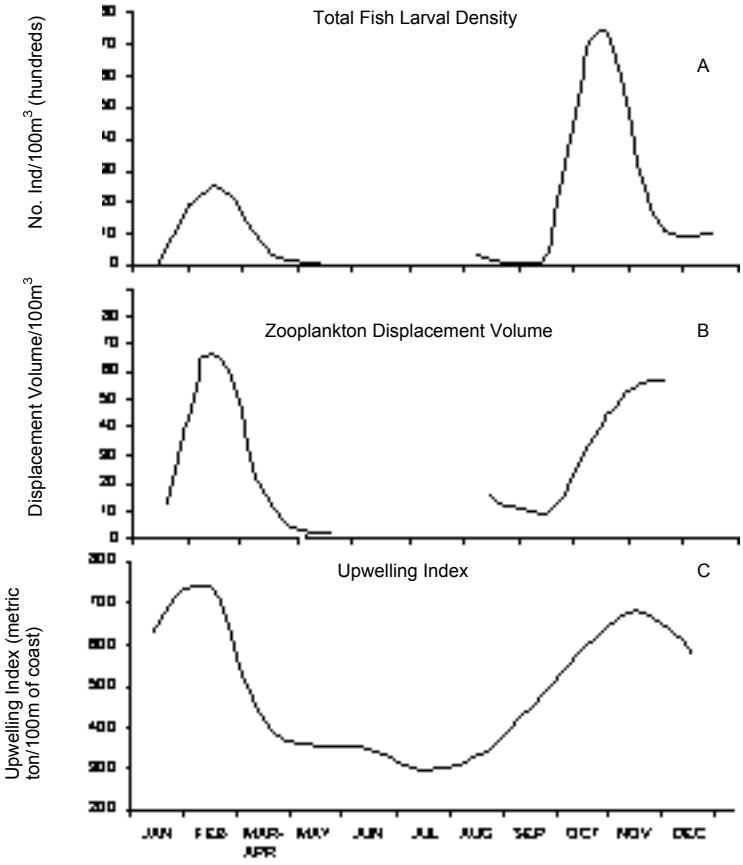

Fig. 7. (A) Total fish larval density (No./100 m^3), (B) zooplankton displacement volume (ml/sample) and (C) upwelling index (metric tons/sec/100 m of coast) during 2000. Upwelling index of waters adjacent to Pisco (15º S-77º W), from Pacific Fisheries Environmental Laboratory-NOAA (http://orpheus.pfeg.noaa.gov/outgoing/upwell/SA/spac 11.15s.mm).

Vertical distributions of larvae in Independencia Bay were well defined; thus larvae apparently are able to maintain vertical position despite the strong vertical mixing suggested by the apparent lack of a thermocline at all four stations throughout the study. Because Hewitt (1980) found essentially no difference in catches of small larvae between a ring and a bongo net, and because most of our larvae were small, we feel justify in making a comparison between the catches from the ring and bongo nets. Overall, more taxa were

caught at the 10 m depth than at the surface, and the classification analyses revealed that depth was more important in distinguishing assemblages than horizontal location, which had little effect on structuring the assemblages. Only one of the nine most abundant taxa, the atherinid, *Odontesthes regia regia*, was consistently most abundant at the surface at all locations; similar neustonic distributions have o been reported for other atherinids, as well (Leis 1991, Schmitt & Leis 2000). The distribution patterns in the bay coincide with those found elsewhere in other studies (Ahlstrom 1959, Boehlert et al 1985, Leis 1991). Larval Blenniidae (*Scartichthys* sp.), Engraulidae (*Engraulis ringens*), Gerreidae (*Eugerres periche*), Gobiesocidae (*Gobiesox marmoratus* and *Tomicodon petersi*), Normanichthyidae (*Normanichthys crockeri*), Paralichthydae (*Paralichthys microps*), Pinguipedidae (*Prolatilus jugularis*), Kyphosidae (*Doydixodon* sp. (*laevifrons* ?)), Labrisomidae (*Labrisomus philippi* (?)), and Haemulidae (*Anisotremus* sp.) were found at least once at the surface in different months, usually at night during the additional sampling (Table 1), but they were never more numerous at the surface than at 10 m depth (Vélez et al., unpublished data). The results of this study are consistent with the hypothesis that fishes in Independencia Bay synchronize their reproductive seasons in response to local environmental factors to take advantage of currents and favorable larval feeding conditions in the bay. Larvae of most species in the bay apparently have a mechanism to stay in the bay (retention), and the coastal pelagic fish larvae (e.g. anchovies, sardines) temporarily use the bay as a nursery area. Those nearshore species which do not complete their life cycles exclusively in embayments (Group III table 10) may time their spawning peaks to coincide with times of reduced currents, and bay species in groups I and II spawn in a pattern that is less dependent upon seasonal current shifts. Because seasonal patterns in primary and secondary productivity in Independencia Bay are poorly documented, and this is the first ichthyoplankton study in the bay, inter-study comparisons are not possible. However, this study shows that the seasonal spawning patterns of adult fish play a key role in the formation of assemblages of early larvae. Future ichthyoplankton studies in the bay should focus on obtaining better resolution of small-scale larval patchiness and links to food and predators.

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Publication II

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Vertical distribution of ichthyoplankton in Independencia Bay, Pisco, Peru

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ABSTRACT

Ichthyoplankton vertical distributions over 24 hours were examined in Independencia Bay, Pisco, Peru. A total of 32 horizontal tows was made at two stations (Panteón and Tunga) of 0 and 10 m depth sampled every three hours during two 24-hour cycles. A total of 4,504 larvae representing 22 families, 25 genera, and 26 species were collected; 99.6% were identified to at least the family level. Larval Blenniidae, Engraulidae, Gobiesocidae, Normanichthyidae, Atherinidae, Pinguipedidae and Labrisomidae accounted for 97.6% of the larvae captured. The number of taxa at the surface was the same (5) at both stations, and was higher at 10 m depth at Tunga (26) than at Panteón (21). Two patterns of larval vertical distribution were observed. Most species were located mainly at 10 m at both stations, but *Odontesthes regia regia* was found mainly at the surface. There were no statistically significant differences between night and day densities of fish larvae at either depth. Nevertheless, a small degree of vertical redistribution was apparent for some species that could be interpreted as nocturnal dispersal or limited directed movement away from daytime concentrations at the surface or 10 m depth. Coupling the larval fish densities of the dominant species to the abiotic factors (temperature, salinity, oxygen, pH and tide) using canonical correspondence analysis (CCA) revealed that hydrographic factors such as temperature, salinity and pH were biologically important. The CCA showed that species-environmental correlations were relatively high for all three axes, ranging from 0.657 for CCA1 to 0.549 for CCA3. The cumulative percentage of species variance (CPSV) accounted for by the CCA totalled 46% for the three CCA axes, and the cumulative percentage of the species-environment relation totalled 29.9% for these axes.

KEYWORDS: ichthyoplankton, fish larvae, vertical distribution, Peru, Pisco, Independencia Bay

INTRODUCTION

Some of the most productive marine regions and largest fish populations are associated with coastal upwelling systems (Cushing, 1969; 1971; Pauli and Tsukayama, 1987), where nutrient-rich deeper waters rise to the ocean surface and support high rates of primary production. A classic example is the Humboldt Current system off western South America. The Peruvian upwelling area is known for extremely rich fisheries and very large populations of small pelagic fish such as anchovies and sardines. This system is characterized by persistently strong south-easterly trade winds, predominantly unidirectional equatorward alongshore surface currents, and persistent offshore-directed surface drift driven by winds, Coriolis force and Ekman transport that results in upwelling near the coast. Independencia Bay is adjacent to the Humboldt Current, and its oceanographic characteristics are influenced by the current. There is little published information on larval fish vertical distributions in Independencia Bay (Vélez et al., 2004) and until now nothing has been known about the structuring effects of larval processes on the fish communities in Independencia Bay. This study was carried out in spring 2000 to describe vertical distributions of larval fish in the bay. Spring is a time of high ichthyoplankton abundance in the bay (Vélez et al., in press), and is the principal spawning time for *Engraulis ringens*, the most important marine resource in Peru. The primary objectives of our study were to determine diel abundance patterns and how these patterns might vary between stations, to determine vertical distributions and densities of fish larvae during the day and at night, and to relate vertical variations of the dominant families during a 24-hour cycle to oceanographic parameters.

METHODS

Study area

Independencia Bay (14º06'-14º20'S; 76º00'-76º18'W), a large, shallow bay situated within the Paracas National Park, Pisco, Peru (Fig. 1), is part of the Paracas National Reserve. It is located in the Humboldt Current marine ecoregion and is a marine upwelling site with high levels of primary production. The bay is about 21 km long and 6.5 km wide, averages 22-25 meters in depth, and has two islands, La Vieja and Santa Rosa. La Vieja Island (5.6 km long and 2.4 km wide) occupies much of the southern half of the mouth of the bay. Tidal mixing with open coastal water and the high run-off of nutrients at La Vieja caused by guano bird colonies are main factors leading to high primary production in Independencia Bay.

Sample collection

Plankton samples were collected in September, 2000, with two nets: a bongo net equipped with 0.505 mm and 0.333 mm mesh nitex nets and cod ends, towed at a depth of 10 meters, and an 0.5 m ring net (0.333 mm mesh nitex) towed at the surface. Both nets were equipped with calibrated flowmeters. All tows were taken at a speed of 3 kn for 10 min. and samples were preserved in 4% formalin solution immediately after collection. In total, 32 horizontal tows were made at two stations, Panteón and Tunga (Fig. 1). Each station was sampled every three hours during a 24-hour period and all sampling was completed during two 24-hour cycles. Operational conditions dictated that samples were only taken from these two depths. In this way, unnecessary damage to the nest by dragging through the sediment or along the sea floor was avoided. Temperature, salinity, pH and dissolved oxygen were measured at four depths (0, 5, 10 and 20 meters) during each collection. Tidal information for the Pisco area was obtained from tidal tables published by HIDRONAV-5023. Sunrise and sunset were determined for local Pacific Daylight Savings Time (PDST) from the nautical atlas (http://aa.usno.navy.mil/data/docs/RS_OneDay.html). In the laboratory, zooplankton biomass was measured using the displacement volume method (Beers, 1976), and all fish larvae were sorted from the samples and identified to the lowest taxon possible. Larvae were identified by the series method, using a combination of meristic and developmental characters that permitted definitive identification. The larvae were stored in 4% formalin.

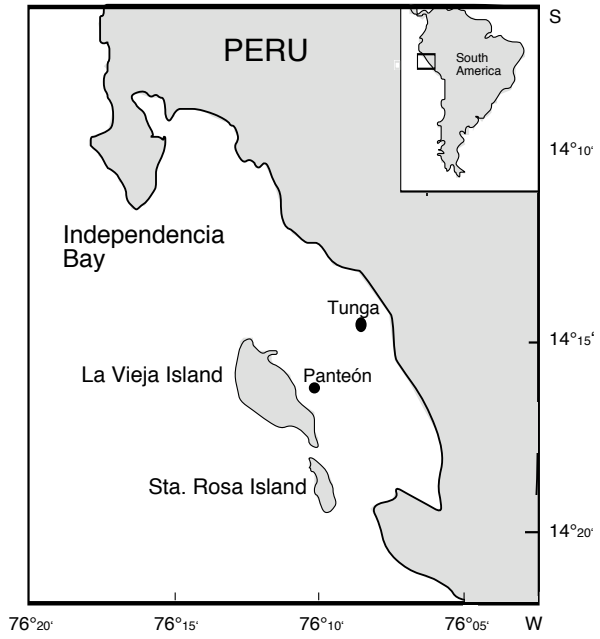

Fig. 1. Study area, Independencia Bay, Pisco, Peru. Sampling locations indicated by black points.

Treatment and Data Analysis

Because some specimens could not be identified to genus or species, abundance data were interpreted at the family level in the quantitative analyses. The six most abundant families at each station were identifiable to species, and four of them contained a single species. Numbers of fish larvae in each tow were standardized to the number per 100 m^3 of water filtered. Densities (larvae/100 m^3) of the seven most abundant taxa (total number of larvae >90) were transformed to log (x+1) prior to statistical testing. All statistical analyses were

based on catches in the 0.333 mm mesh samples from both depths. The null hypothesis of no difference between stations or strata was evaluated at a significance level of $p \leq 0.05$. We used a three-factor analysis of variance (ANOVA) with the following factors: Station (Panteón vs Tunga), depth (surface vs 10 meters), and time (day vs night). The PC-ORD for windows (McCune et al., 1999) was used for a canonical correspondence analysis (CCA) (Ter Braak, 1986). The CCA was used to examine the relationships of variations in density of the dominant species and environmental variables.

RESULTS

Environmental variables

The tide in the bay is mixed semi-diurnal, with two highs and two lows daily. In general, vertical similarities in temperature (Figs. 2A, 2B) and salinity (Figs. 2C, 2D) reflect the extent of vertical mixing in Independencia Bay. Each environmental parameter tended to follow a similar diel pattern at each of the four depths. Surface water temperatures at Panteón ranged from 13.8°C (0:00 hours) to 14.5°C (during most of the day) with an average of 14.3°C, and gradually decreased to 13.4-14.0 °C (average 13.6°C) at 20 m depth (Fig. 2A). At Tunga (Fig. 2B) the temperatures were a bit higher, ranging from 13.6-15.5°C (average 14.6°C) at the surface and gradually declining to 13.4-14.1°C (average 13.7°C) at 20 m depth. Vertical thermal profiles were remarkably similar at both stations and day-time solar heating was apparent at both stations. Salinity at Panteón ranged between 32.9 and 33.0 ppt at the surface and displayed a similar diel pattern at all four depths (Fig. 2C). At Tunga, the salinity values (Fig. 2D) varied between 32.5 and 33.0 ppt and also displayed similar trends at all depths. A small, but distinct depression in salinity at both stations corresponded with the afternoon low tide, but otherwise there was little evidence of a tidal influence on salinity. Dissolved oxygen values at Panteón (Fig. 2E) ranged between 2.21 ml/l (20 meters) and 6.97 ml/l (5 meters). At the surface, the dissolved oxygen tended to be slightly lower at night than during the day. Subsurface dissolved oxygen levels tended to be as high as, or higher than surface values (Fig. 2E). The dissolved oxygen values at Tunga (Fig. 2F) varied between 3.42 and 7.6 ml/l in the upper 5 m, and usually were distinctly lower at 10 and 20 m, ranging between 1.91 and 6.68 ml/l (Fig. 2F). There was scant evidence of a tidal influence on dissolved oxygen levels apart from a slight elevation at all depths at Panteón during the afternoon low tide, and a tendency for values to be reduced during tidal reversals at Tunga. The pH values at Panteón (Fig. 2G) varied little with depth or through time, ranging between 7.77 and 7.88 (average 7.83). Values likewise varied little at Tunga, ranging from 7.54 to 7.94 (average 7.79) (Fig. 2H).

Canonical correspondence analysis

The CCA was used to see to what extent the patterns of variation in densities of the dominant taxa could be explained by the environmental variables measured, and to aid in visualizing the centers of the species density distributions along each environmental variable. Eigenvalues, measures of importance for CCA axes that may vary between zero and one, were relatively low for all three axes (Table 1). However, species-environmental correlations were relatively high for all three axes, ranging from 0.657 for CCA 1 to 0.549 for CCA 3. The cumulative percentage of species variance (CPSV) accounted for by the CCA totalled 46% for the three CCA axes, and the cumulative percentage of the species-environment relation totalled 29.9% for these axes. The five environmental variables were evaluated through their inter-set correlations (Tables 2 and 3).

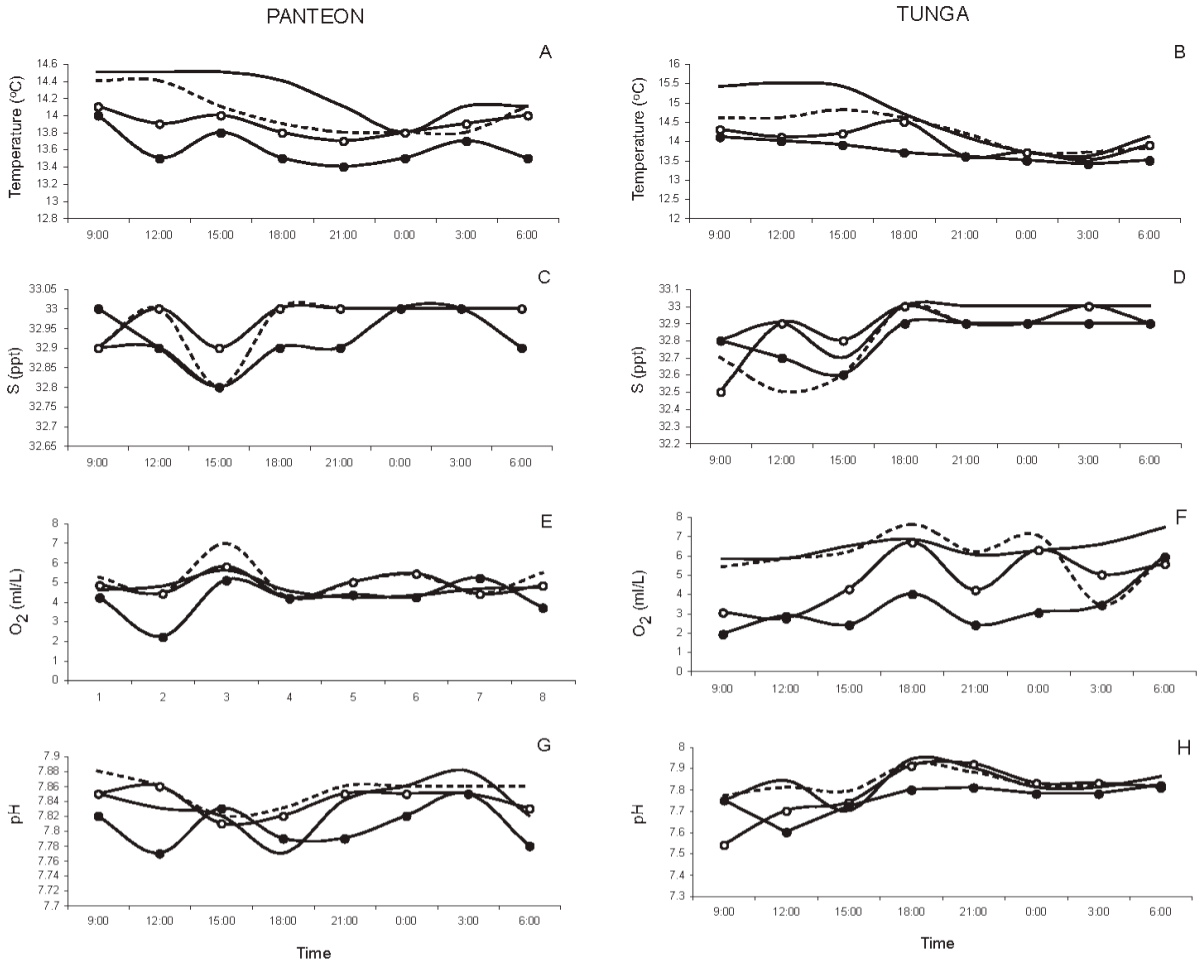

Fig. 2. Mean values for temperature (A, B), salinity (C, D), oxygen (E, F), pH (G, H) at four depths (0, 5, 10 and 20 m) at Panteón and Tunga in spring 2000. Solid line=0 m, dashed line=5m, open circle=10 m, filled circle=20 m.

Table 1. Results from canonical correspondence analysis (CCA) for the dominant taxa from Independencia Bay.

	CCA axes			
	1	2	3	Total inertia
Eigenvalues	0.260	0.142	0.074	1.5936
Variance in sp data (% of variance explained)	16.3	8.9	4.6	
Cumulative % explained	16.3	25.3	29.9	
Pearson correlation, spp-Envt*	0.657	0.553	0.549	

Correlation between sample score for an axis derived from the species data and the sample scores that are linear combinations of the environmental variables. Set to 0.000 if axis is not canonical.

An environmental variable having an inter-set correlation ≥ 0.35 was considered biologically important. Based on this criterion, three variables were regarded as important correlates of one or more axes (Table 3). Gradients in some physical conditions, like temperature and salinity, were correlated with the densities of the dominant taxa in the CCA (Table 2).

Table 2. Canonical (regression) coefficients for the standardized environmental variables.

Variable	CCA axis 1	CCA axis 2	CCA axis 3
Tide	-0.225	-0.297	-0.287
Temperature	0.930	0.737	-0.316
Salinity	0.052	1.639	-0.443
Oxygen	0.319	-0.286	0.556
pH	0.006	-0.649	0.893

Table 3. Inter-set correlations of the environmental variables with canonical correspondence analysis (CCA) axes. Bold values denote those variables that were considered to be biologically meaningful for the CCA axis.

	Correlations		
Variable	**CCA axis 1**	**CCA axis 2**	**CCA axis 3**
Tide	-0.045	-0.111	-0.187
Temperature	**0.615**	-0.006	-0.164
Salinity	-0.279	**0.390**	0.267
Oxygen	0.279	-0.119	0.310
pH	-0.109	0.230	**0.436**

Zooplankton biomass

Standardized zooplankton displacement volumes were similar at the surface for both stations (Figs. 3), but were higher at 10 m at Tunga (average=32.75 ml) than at Panteón (average=15.25. Surface values at Panteón increased during the day to a maximum of 11 ml at 18:00 hours, with a nocturnal average of 6.4 ml and a daytime average of 2.8 ml. At Tunga, the surface value also peaked at 18:00 hours (16 ml), with a night-time mean value of 5.9 ml and a day-time mean of 3.1 ml. The displacement volume at 10 m depth at Tunga was highest at 00:00 hours (40 ml); the nocturnal average was 31.5 ml/sample and the day-time average 34 ml/sample. At Panteón displacement volume at 10 m was highest at 18:00 hours (19 ml), with the same day and night average (15.25 ml). There was little indication of a tidal influence on zooplankton volumes (Figs. 4-5).

Taxonomic composition of the ichthyoplankton

4,504 larvae representing 22 families, 25 genera, and 26 species were collected, of which 99.6% were identified to at least the family level. Most larvae not identified to family (0.5%) were yolk-sac stage (7 larvae of two types), or unidentifiable damaged larvae (11

individuals). Only a small proportion of the taxa contributed significantly to the total abundance of fish larvae; most were rare. In general, each of the rare taxa occurred in less than 0.04% of the samples. Blenniidae, Engraulidae, Gobiesocidae, Normanichthyidae, Atherinidae and Labrisomidae comprised 97.6% of the larvae captured at Panteón. Gobiesocidae, Atherinidae, Pinguipedidae, Blenniidae, Engraulidae, and Labrisomidae comprised 77.6% of the larvae captured at Tunga (Table 4).

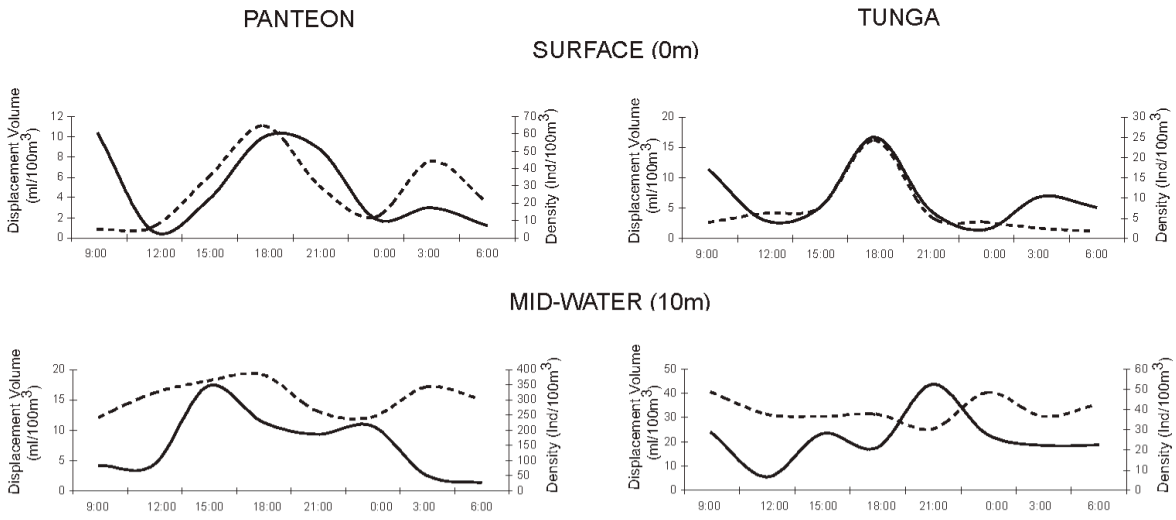

Fig. 3. Zooplankton displacement volume (dashed line) and density of fish larvae (solid line) at Panteón and Tunga at the surface (0 m) and mid-water (10 m) during the 24-hour cycle. Comparisons include only the 300 micrometer samples from both depths.

Distributions and abundances of larval fishes

Total larval density and abundance were higher at Panteón than at Tunga. Both abundance and number of taxa increased between 12:00 and 21:00 hours at both stations (Table 5). Abundance at Panteón peaked at 15:00 hours, reflecting a large catch of *Scartichthys* sp. at that time (412 Ind/100 m^2), and changed little between 18:00 and 00:00 hours. The number of taxa at Panteón was lowest in the morning and reached a maximum at 21:00 hours (Table 5). Both abundance and number of taxa at Tunga peaked at 21:00 hours (Table 5). Species composition did not vary substantially between 18:00 and 3:00 hours: we found 84.6% and 75% of the total taxa at Panteón and Tunga, respectively, during this period. At the surface, overall larval density usually was highest at night (18:00-03:00 hours) at Panteón, but less clearly so at Tunga (Table 5). The overall larval density at 10 m depth at Panteón was higher at night, apart from the highest value at 15:00 hours reflecting the large collection of *Scarthichthys* sp. Overall larval density at 10 m depth at Tunga differed relatively little between day and night (Table 5).

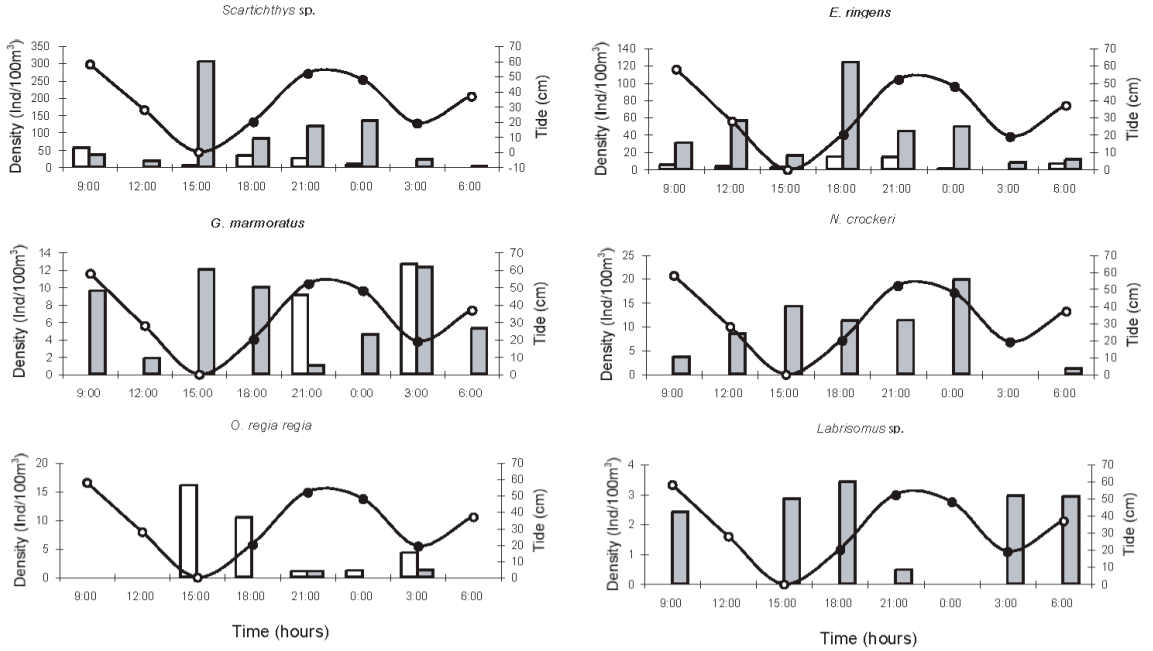

Fig. 4. 24-hour cycle distributions of the most abundant ichthyoplankton taxa collected at Panteón. The solid lines indicate tide height. Filled circles denote night and open circles denote day. Open bars= surface, shaded bars=10 m. Note that the density scales differ between species.

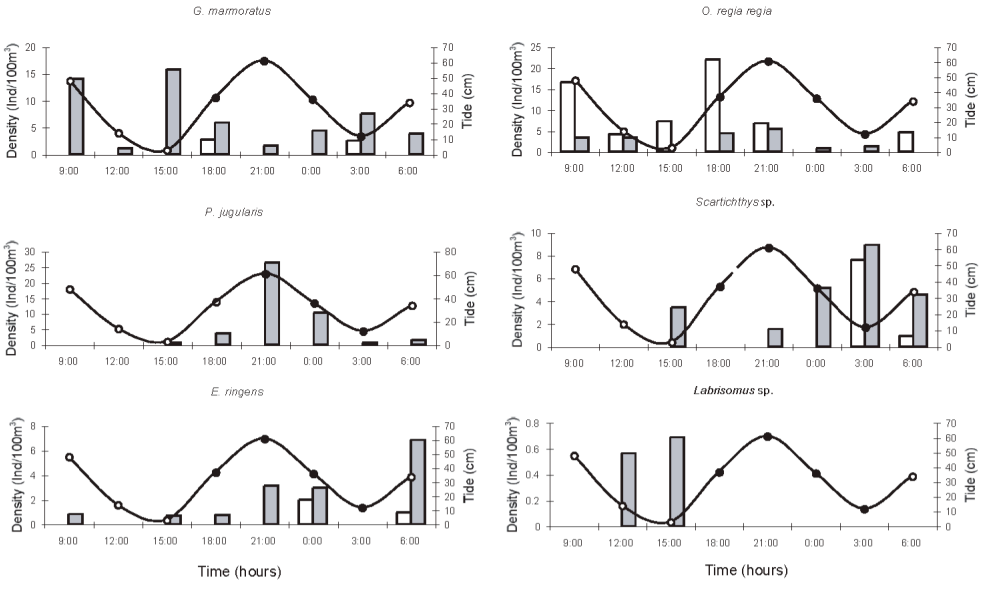

Fig. 5. 24-hour cycle distributions of the most abundant ichthyoplankton taxa collected at Tunga. The solid lines indicate tide height. Filled circles denote night and open circles denote day. Open bars= surface, shaded bars=10 m. Note that the density scales differ between species.

Vertical distributions and 24-hour trends in the abundances of the dominant species

Larval densities differed significantly between depths for all of the dominant taxa (Table 6). The ANOVA showed significant depth effects for all seven taxa and significant interactions between station and depth for four dominant taxa (Table 6); the interaction approached

significance for another (*Labrisomus* sp., p= 0.08). There were no significant differences in abundances between day and night for any of the dominant taxa (Table 6), although the difference for *P. jugularis* approached significance (p= 0.09). There were no significant interactions between stations and time (day or night), although the interactions approached significance for *Labrisomus* sp. and *P. jugularis* (p=0.08 and 0.09, respectively). There also were no significant interactions between depth and time (day or night), although the interactions approached significance for *G. marmoratus* (p=0.06), and *P. jugularis* (p=0.09). There were no significant three-way interactions between station, depth and time (Table 6). Vertical distributions of the most abundant taxa at both stations are summarized in Table 7, which shows clearly that more individuals, except the Atherinidae (*O. regia regia*), were captured at 10 m.

Table 4. Total numbers (N), percent contribution (D) and frequency (F) of capture of the ichtyoplankton collected at the two stations at Independencia Bay during 2000.

		PANTEON			TUNGA			OVERALL		
Family	**Genus /Species**	**N**	**D**	**F**	**N**	**D**	**F**	**N**	**D**	**F**
Atherinidae	*Odontesthes regia regia*	36	0.9	62.5	91	16.6	100	127	2.8	81.25
Blenniidae	*Scartichthys* sp.	2417	61.1	100	38	6.92	75	2455	54.5	87.5
	Hypsoblennius sp. *(robustus? sordidus?)*	40	1.0	75	14	2.6	62.5	54	1.2	68.75
Carangidae	*?*	2	0.05	12.5	0	0	0	2	0.044	6.25
Centropomidae	*?*	1	0.025	12.5	0	0	0	1	0.022	6.25
Chaenopsidae	*Emblemaria* sp. *(hudsoni? tortugae?)*	0	0	0	2	0.36	25	2	0.044	12.5
Engraulidae	*Engraulis ringens*	920	23.3	100	28	5.1	100	948	21.04	100
Gerreidae	*Eugerres periche*	9	0.23	12.5	0	0	0	9	0.2	6.25
Gobiesocidae	*Gobiesox marmoratus*	220	5.6	87.5	161	29.3	100	381	8.4	93.75
Gobiidae	*Evermannia zostetura*	2	0.05	25	1	0.18	12.5	3	0.07	18.75
Haemulidae	*Anisotremus (dovi? scapularis?)*	5	0.13	37.5	11	2	62.5	16	0.35	50
Labridae	*(Bodianus? Halichoeres?)*	0	0	0	1	0.18	12.5	1	0.022	6.25
Labrisomidae	*Labrisomus (philippii?)*	60	1.52	87.5	36	6.5	87.5	96	2.13	87.5
Nomeidae	*Nomeus gronovi*	0	0	0	1	0.18	12.5	1	0.022	6.25
Normanichthyidae	*Normanichthys crockeri*	210	5.31	100	19	3.5	75	229	5.0	87.5
Ophidiidae	*?*	0	0	0	2	0.36	25	2	0.044	12.5
Paralichthyidae	*Paralichthys adspersus*	4	0.1	37.5	8	1.46	25	12	0.27	31.25
	P. microps	0	0	0	10	1.82	25	10	0.22	12.5
	Etropus ectenes?	6	0.15	37.5	0	0	0	6	0.13	18.75
	Hippoglossina	1	0.025	12.5	0	0	0	1	0.22	6.25
Pinguipadidae	*Prolatilus jugularis*	0	0	0	108	19.7	87.5	108	2.4	43.75
Pomacentridae	*Chromis* sp.	5	0.13	37.5	0	0	0	5	0.11	18.75
Sciaenidae	*Sciaena (fasciata? starksi?)*	0	0	0	3	0.55	12.5	3	0.07	6.25
Scombridae	*Auxis* sp.	0	0	0	2	0.36	25	2	0.044	12.5
Scorpaenidae	*Sebastes capensis*	8	0.20	50	2	0.36	25	10	0.22	37.5
Syngnathidae	*Leptonotus blainvillianus*	0	0	0	2	0.36	25	2	0.044	12.5
Unidentified		9	0.23	50	9	1.64	50	18	0.4	50

DISCUSSION

The ichthyofauna of Independencia Bay was relatively rich but was dominated by a few abundant species: only a small proportion of the total taxa (26.9%: 7 taxa) contributed most

of the total abundance (97.6% at Panteón and 77.6% at Tunga). The assemblages of larval fishes at both stations were comprised of similar taxa.

Table 5. Total number of individuals, total number of taxa, and densities (N/100 m^3) at the surface and mid-water at the two stations. The totals are also shown.

TIME	SURFACE			MID-WATER			TOTAL		
PANTEÓN	**N**	**Taxa**	**D**	**N**	**Taxa**	**D**	**N**	**D**	**Taxa**
09:00	48	2	60	171	7	96	219	156	7
12:00	2	1	3	223	7	118	225	121	7
15:00	19	3	22	1123	9	483	1142	505	10
18:00	56	3	58	539	10	254	595	312	11
21:00	50	5	51	626	13	272	676	323	13
00:00	9	3	10	703	11	327	712	337	11
03:00	12	2	17	182	10	85	194	102	10
06:00	5	1	7	187	8	76	192	83	8
Total	**201**	**5**	**228**	**3754**	**21**	**1711**	**3955**	**1939**	
TUNGA	**N**	**Taxa**	**D**	**N**	**Taxa**	**D**	**N**	**D**	**Taxa**
09:00	20	1	17	73	14	45	93	62	14
12:00	5	1	4	20	6	10	25	14	6
15:00	4	1	7	76	11	46	80	53	11
18:00	9	2	25	71	12	44	80	69	12
21:00	1	1	7	107	16	73	108	80	16
00:00	1	1	2	48	11	33	49	35	11
03:00	4	2	10	50	9	23	54	33	9
06:00	8	4	7	52	10	33	60	40	12
Total	**52**	**5**	**79**	**497**	**26**	**307**	**549**	**386**	

Overall, more taxa were caught at 10 m depth than at the surface, and larval densities were higher at 10 m depth for most taxa (Tables 3, 4). Although no statistically significant redistributions suggestive of vertical migration were detected, inspection of the data reveals some evidence of dispersal or limited movement away from daytime abundance centers for some taxa (Figs. 6 and 7). Surface/10 m ratios of larval densities suggest that the atherinid, *O. regia regia*, is concentrated at the surface at both stations during the day, and disperses to some extent at night (Fig. 7), possibly as a result of reduced nocturnal activity. *G. marmoratus*, in contrast, was most abundant at 10 m depth, and apparently avoided the surface during the daytime at both stations, but was present at the surface at night. The lack of larvae at the surface during the day could result from active downward migration or passive sinking, or it could be explained by visual avoidance of the surface net. Most of the *G. marmoratus* caught in this study were small, preflexion and flexion stages, and are unlikely to have been very successful in avoiding the surface net. Thus it seems more plausible that the complete lack of larvae in the surface samples during the day reflects a real lack of larvae there rather than significant avoidance of the surface net. The presence of larval *G. marmoratus* at the surface at night suggests that at least some fraction of the larvae ascend in the water column during the night. At Panteón, *Scartichthys* sp. larvae were slightly more concentrated at depth during the day than at night, possibly suggesting some limited

movement. At Tunga *E. ringens* were more concentrated at depth during the day than at night, but at Panteón they were not, and this difference simply could be a chance occurrence. *Labrisomus* sp., *P. jugularis*, and *N. crockeri* did not occur at the surface and thus showed no evidence of vertical movement in the upper 10 m. Larger day time catches of *Labrisomus* sp. suggest the possibility that it may tend to migrate or settle from mid-water into the epibenthic layer at night, as has been shown for another labrisomid, *Paraclinus integripinnis* (Barnett et al., 1984). The samples were collected on moonlit nights near full moon, and larval distributions may differ on dark nights, for example bright moonlight may facilitate night-time concentrations of *Odontesthes* larvae at the surface. It is possible, too, that moonlight may result in increased avoidance of the surface net.

Larval abundance in relation to environmental conditions

The larval fish densities were most strongly related to temperature in Independencia Bay, with slightly less strong correlations with salinity and pH. However, the correlations between the densities and other environmental variables were low or not significant, probably as a result of the small number of samples available for this study. Although the correlation with temperature might be interpreted as evidence for larval preference for a certain temperature range, the fact that temperature has the strongest vertical gradient among the physical variables measured, and the fish larvae all have strong vertical differences in abundances, may mean instead that the observed correlation is coincidental. In many bays and estuaries, small-scale tidal fronts and tidal phase may influence patterns of ichthyoplankton distribution (Vargas et al., 2003). However, there is relatively little evidence, based on our limited study, that this is the case in Independencia Bay. Although no clear, general relationship between larval distributions and tidal phase was observed, densities of some taxa, for example *P. jugularis* at Tunga, *Scartichthys* sp. at Panteón, and *E. ringens* at both stations, tended to be higher on rising or high tide and lower near low tide. However, owing to our limited data set, we can suggest the possibility of a relationship with tide for some taxa, but cannot demonstrate it. The few small vertical redistributions observed apparently were unrelated to tidal phase. Vertical distributions of larvae in Independencia Bay were well defined; thus larvae apparently are able to maintain their vertical position despite the vertical mixing suggested by the apparent lack of a strong thermocline at both stations. This agrees with results of a more extensive survey in the bay (Vélez et al., 2004) that revealed that depth was the most important factor in distinguishing ichthyoplankton assemblages. Future ichthyoplankton studies in the bay should focus on obtaining a better resolution of depth including the near-bottom stratum, and more extensive sampling spatially and/or temporally to better define vertical patterns.

Table 6. Summaries of ANOVAs on the dominant taxa. Mean square values (rounded to two decimals=MS; *=p ≤ 0.05; **= p < 0.01; NS=not significant, p > 0.05.

Source of	(d)	*Scartichthys* sp.			*Engraulis ringens*			*Gobiesox marmoratus*			*Normanichthys. crockeri*			*Odontesthes. regia*			Labrisomus sp.			*Prolatilus. jugularis*		
Variation	1	MS	F	P	MS	F	p	MS	F	P	MS	F	P	MS	F	P	MS	F	P	M	F	P
Station (St)	1	0.11	13.85	**	0.03	21.31	**	1.3E-04	0.59	NS	0.001	6.09	*	0.001	2.05	NS	4.6E-05	3.25	NS	0.001	6.59	*
Depth (D)	1	0.04	4.49	*	0.01	9.35	**	0.002	8.89	**	0.002	15.56	**	0.003	6.80	*	1.5E-04	10.75	**	0.001	6.59	*
Time (T)	1	0.00	0.18	NS	0.002	1.67	NS	1.1E-04	0.47	NS	1.5E-04	1.20	NS	1.0E-05	0.02	NS	6.8E-08	0.01	NS	3.0E-4	3.09	NS
St x D	1	0.03	4.23	*	0.01	7.87	**	1.5E-04	0.63	NS	0.001	6.09	*	1.1E-04	0.24	NS	4.6E-05	3.25	NS	0.001	6.59	*
St x T	1	0.00	0.06	NS	0.002	1.71	NS	0.001	2.72	NS	1.1E-06	0.01	NS	1.7E-06	0.00	NS	8.6E-07	0.06	NS	3.0E-4	3.09	NS
D x T	1	1.1E-04	0.01	NS	0.001	0.57	NS	0.001	3.74	NS	1.5E-04	1.20	NS	6.8E-05	0.15	NS	6.8E-08	0.01	NS	3.0E-4	3.09	NS
St x D x T	1	2.0E-04	0.03	NS	0.001	0.75	NS	1.6E-06	0.01	NS	1.1E-06	0.01	NS	5.9E-05	0.13	NS	8.6E-07	0.06	NS	3.0E-4	3.09	NS
Residual	24	0.20	0.01		0.03	0.00		2.3E-04	0.59		0.003	0.00		4.5E-04	2.05		1.4E-05	3.25		9.8E-5		

Table 7. Catches (No./100m^3) of dominant taxa in both stations at Independencia Bay in 2000 during each time sampled.

Total catch, dominance (% contribution to the overall total), percent in upper and lower region of the water column and adult habitats (N=neritic; B=benthic; CP=coastal pelagic) are also shown.

DOMINANT TAXA	TIME (HOUR OF THE DAY)												
PANTEÓN	**09:00**	**12:00**	**15:00**	**18:00**	**21:00**	**00:00**	**03:00**	**06:00**	**TOTAL CATCH**	**D**	**% SURFACE**	**% MIDWATER**	**ADULT HABITAT**
Scartichthys sp.	90	29	412	133	190	216	39	45	1154	61	10.8	89.2	B
Engraulis ringens	41	78	25	144	82	73	9	15	467	25	10.1	89.1	CP
Gobiesox marmoratus	17	2	12	0	20	11	37	10	109	6	20	80	B
Normanichthys crockeri	6	11	22	12	17	28	1	2	99	5	0	100	N
Odontesthes regia regia	0	0	16	11	3	2	6	0	38	2	91	9	N
Labrisomus sp.	3	0	8	5	1	1	8	4	30	2	0	100	B
TUNGA	**09:00**	**12:00**	**15:00**	**18:00**	**21:00**	**00:00**	**03:00**	**06:00**	**TOTAL CATCH**	**D**	**% SURFACE**	**% MIDWATER**	**ADULT HABITAT**
Gobiesox marmoratus	27	2	21	13	4	7	11	11	96	28	5.6	94.4	B
Odontesthes regia regia	20	10	8	31	15	2	3	5	94	28	69.7	30.3	N
Prolatilus jugularis	1	0	7	15	33	11	1	3	71	21	0	100	B
Scartichthys sp.	4	0	1	1	2	5	17	6	36	10	25.3	74.7	B
Engraulis ringens	1	1	1	1	4	5	1	9	23	6	13.9	86.1	CP
Labrisomus sp.	5	1	6	2	4	0	2	2	22	6	0	100	B

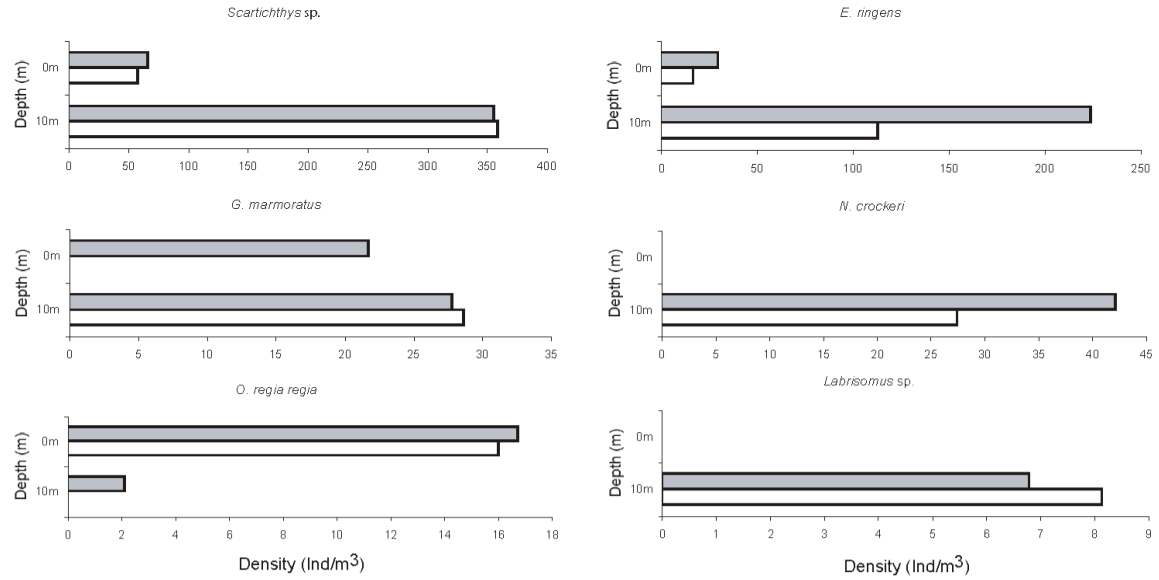

Fig. 6. Day and night densities of the most abundant ichthyoplankton taxa collected at Panteón at 0 and 10 m depth. Note that the density scales differ between species; shaded bars denote night and open bars denote day.

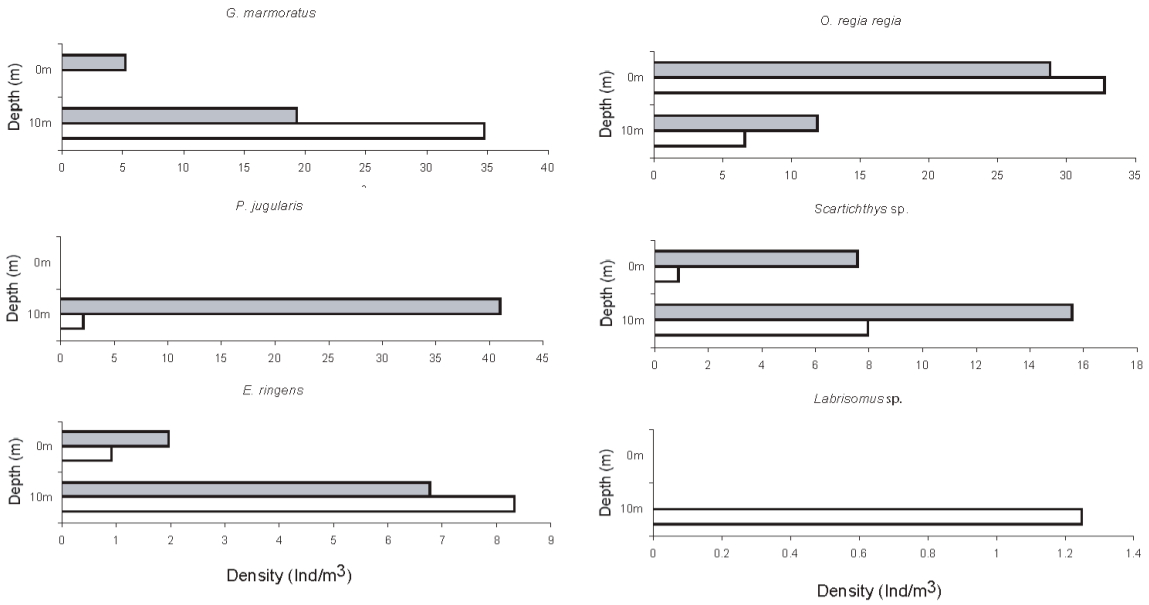

Fig. 7. Day and night densities of the most abundant ichthyoplankton taxa collected at Tunga at 0 and 10 m depth. Note that the density scales differ between species; shaded bars denote night and open bars denote day.

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Publication III

Larval and osteological development of the Mote Sculpin *(Normanichthys crockeri)* (Pisces:Normanichthyidae) from the Independencia Bay, Pisco, Peru.

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Larval and osteological development of the mote sculpin (*Normanichthys crockeri)* (Pisces:Normanichthyidae) from the Independencia Bight, Pisco, Peru

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Ontogeny of Normanichthys crockeri is described and illustrated based on 66 specimens (1.9–20.5 mm; including recently hatched larvae through to the transformation stage) collected in Bahia Independencia, Pisco, Peru. Larvae hatch at approximately 1.8 mm, undergo notochord flexion at ca. 6.2–9.0 mm, and transform to juveniles at ca. 20.0 mm. Larvae were identified by the series method, using a combination of meristic and developmental characters that permitted definitive identification. Diagnostic features of the larvae include early development of large, lightly pigmented pectoral fins; early dorsal midline pigment on the trunk and tail which decreases gradually to none by the beginning of the flexion stage and does not reappear until late postflexion stage; and pigment ventrally, on the midlines of the abdominal and postanal regions, on the preanal until late postflexion stage, at the angular, on the caudal region, and usually at the cleithrum. Larvae are moderately slender with preanal length roughly half of body length (ca. 40–53% body length). They have I,5 pelvic-fin rays, 7+6 principal caudal-fin rays and 36–37 myomeres (11–13+24–26, usually 13+24). The cleithra and bones of the jaws and opercular series are among the first to begin ossifying. The anterior vertebrae begin to ossify at ca. 5.0 mm and addition is posteriorly. The pectoral fin is the first to begin ray formation, followed sequentially by the principal caudal-fin rays, second dorsal- and anal-fin rays (forming concurrently), spiny dorsal-fin rays, and pelvic-fin rays.

INTRODUCTION

Marine fish diversity in Peru is high and the larval stages of many taxa are poorly known. An abundant coastal species, *Normanichthys crockeri* Clark, 1937 is a small (maximum ca. 11.0 cm), schooling, pelagic fish endemic to the southeast Pacific from Chimbote, Peru to Isla Mocha, Chile. *Normanichthys* grazes on aquatic plants and feeds on small fish, zooplankton and phytoplankton; its mode of reproduction and eggs are unknown. This species, commonly known as mote sculpin or camotillo (Clark, 1937), is not commercially important, and thus has been the subject of relatively little research.

There has been considerable disagreement among authors concerning the taxonomic placement of the monospecific family Normanichthyidae. *Normanichthys* has been allied with the cottoid fish (Clark, 1937; Norman, 1938; Fowler, 1951; Berg, 1947; Greenwood *et al.*, 1966), placed in its own scorpaeniform suborder, Normanichthyoidei (Nelson, 1994; Eschmeyer, 1998), and considered '*incertae sedis*' in the Scorpaeniformes (Balbontín and Pérez, 1980; Washington *et al.*, 1984b; Mandrytza, 1991; Vegas and Pequeño, 1993; Yabe and Uyeno, 1996). Here we follow Eschmeyer (Eschmeyer, 1998), in placing *N. crockeri* in the scorpaeniform suborder Normanichthyoidei, but we note that a feature of its skeletal development suggests the possibility that its phylogenetic relationships are outside the Scorpaeniformes.

Larval *N. crockeri* were described and illustrated by Balbontín and Pérez (Balbontín and Pérez, 1980), based on a series of 19 specimens (4.16–16.3 mm), and Washington *et al.* (Washington *et al.*, 1984a) provided an illustration and brief discussion of the larval features. Developmental osteology was not included in either of

these studies. Our decision to re-describe *N. crockeri* was based on a more complete ontogenetic series (1.9–21.7 mm) and larger number (5155) of specimens available to us than were available in the earlier studies. We provide here a re-description of development from just after hatching through transformation to the juvenile stage, including new information about hatching size, and larval morphology, pigmentation and some aspects of osteological development, to supplement the work of Balbontín and Pérez (Balbontín and Pérez, 1980) and to facilitate identification of this species in ichthyoplankton samples.

METHOD

Larval *Normanichthys crockeri* were collected during eight monthly surveys (January–March, May, August–November) in 2000 in Independencia Bight (14°06′–14°20′S; 76°00′–76°18′W), a shallow bight (average depth 20–25 m) in Pisco, Peru. Plankton was collected with a 60 cm, non-closing bongo net equipped with 0.333 mm and 0.505 mm nitex mesh nets and cod ends, towed at a depth of 10 m, and with a 0.5 m ring net (0.333 mm nitex mesh) towed at the surface; both nets were equipped with calibrated flow meters. All tows were taken at speeds of 3 km for 10 min and samples were preserved in 4% formalin immediately after collection. Totals of 56 horizontal tows were made at each depth at four stations (Figure 1). All sampling was carried out during daylight hours except during September, when samples were taken every 3 h during a 24 h period at two of the stations (Panteon and Tunga) (Figure 1).

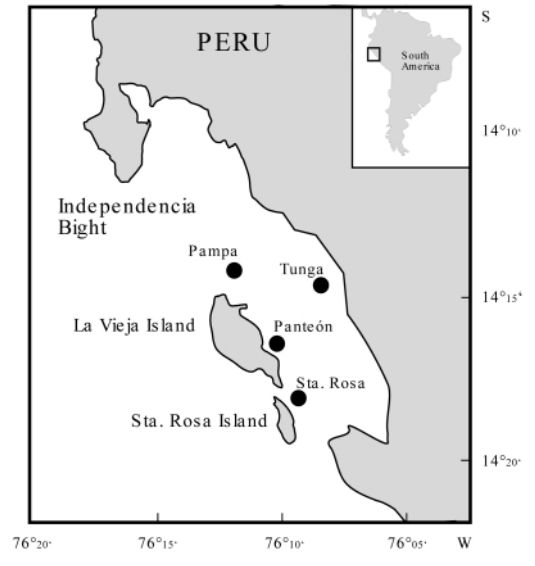

Fig. 1. Study area; Independencia Bight, Pisco Peru. Sampling locations are indicated by black circles. Average depth 20–25 m.

In the laboratory all fish larvae were sorted from the samples and identified to the lowest taxon possible. The larvae were stored in 4% formalin. A total of 5155 larval *N. crockeri* (1.9–21.6 mm body length) were identified, 66 were selected for description, of which forty-four larvae (2.7–20.6 mm) were deposited at the Zoological Institute and Zoological Museum, University of Hamburg (ZHM-9394 to ZHM-9397); nineteen larvae (7.3–14.0 mm) and five adult specimens ranging in size from 59.3 to 71.8 mm were obtained from the Marine Vertebrates Collection of SCRIPPS Institution of Oceanography (SIO 83-147 and SIO 01-75); these specimens had been collected from San Vicente Bight, Chile.

Larvae were identified by the series method, using a combination of meristic and developmental characters that permitted definitive identification. We used only specimens in good condition, which were measured to the nearest 0.02 mm with the ocular micrometer of a dissecting microscope. Measurements were completed within 1.5 years after collection. Methods of counting and landmarks for measurements are defined by Moser and by Leis and Carson-Ewart (Moser, 1996; Leis and Carson-Ewart, 2000). Body parts measured include: Body Length (BL), Snout–Anus Length (Sn-A), Body Depth (BD), Head Length (HL), Head Width (HW), Snout Length (SL), Eye Diameter (ED), Pectoral Fin Length (P_1L) and Pelvic Fin Length (P_2L). In the following description larval lengths always refer to body length. The morphometric series served as the basis for descriptions of the pigment pattern. Description of pigmentation refers solely to melanophores. Six specimens (ZHM-9394) were illustrated, to show pigmentation characters and morphological changes, and to provide identification of all stages of development of *N. crockeri*. Eight specimens (ZHM-9395) ranging from preflexion to late transformation stage were cleared with potassium hydroxide and stained with Alizarin red-S, to observe ossification of the jaws, suspensorium and opercular series bones, axial skeleton, appendicular skeleton, and fins. Staining procedures followed Potthoff (Potthoff, 1984). Skeletal structures were considered ossified upon uptake of Alizarin red-S stain. Twenty-four specimens ranging from postflexion to adult were selected for radiography to obtain more accurate meristic counts.

RESULTS

Morphology

Larvae hatch at a small size: our smallest specimen was 1.8 mm BL. Based on its relatively undifferentiated stage of development, this specimen appeared to have hatched recently, but it had no remaining yolk. Notochord flexion

begins between about 6.2 and 7.0 mm and ends at about 9.0 mm, and transformation to the juvenile stage begins at ca. 20.0 mm and is completed by about 22.0 mm.

Larvae elongate and slender (Figures 2, 3): BD averages 13% BL in the preflexion stage, increasing to 19% in the transformation stage, and decreasing to 17% in adults. Sn-A distance is 40–53% BL throughout larval development, increasing to 59% in adults (Table I). Head is relatively small, initially rounded but becomes more wedge-shaped as snout elongates (by ca. 3.0 mm). Head length is 17–31% BL through most of the larval period, increasing to 34% during transformation. Larvae become compressed: head width decreases from 60% HL in early larvae to 38% in transforming larvae through to adult. Eye diameter in preflexion stage is about 38% HL, decreases to ca. 27% and 22% HL in early flexion and postflexion larvae, respectively, and to 20% HL by transformation. Pectoral fin length increases from 2% BL early in preflexion stage (1.9 mm) to 14% BL late in stage (6.2 mm), to 20% and 29% BL in flexion and postflexion stages, respectively, and to 26% in transformation stage (Table I).

Pigmentation

Head pigment is usually absent in preflexion and flexion stages; we observed internal hindbrain pigment in two specimens (5.7 mm, 7.8 mm). Head pigment usually first appears internally at hindbrain during postflexion stage (ca. 9.2 mm) and externally over midbrain area (by ca. 16 mm); increases internally and externally (Figure 3B). During transformation much of the dorsal surface of the head becomes pigmented. Lower lip and snout pigment does not usually appear until near the end of postflexion stage (15.2 mm), although a single pigment spot was observed at the lower lip in two specimens (10.3 mm, 10.5 mm). During transformation pigmentation forms and increases between the eyes, on the snout, and on the mandibular region (Figure 3B, C). The gular region has a single ventral pigment spot during preflexion stage (Figure 2A, C); one to three spots at angular during all stages. Ventral pigment appears in the branchiostegal region in late preflexion stage (ca. 5.7 mm). A single melanophore usually develops on or under the gill cover during the flexion stage (Figure 2C–E) and more are added during transformation (Figure 3B, C).

The most conspicuous pigment in early larvae is a single dorsal midline row of 3–13 melanophores on the trunk and tail. The number of dorsal melanophores gradually decreases during preflexion stage: a 3.3 mm larva had 13 melanophores and a 6.1 mm larva had only three. Dorsal pigment is absent by the beginning of the flexion stage (ca. 7.0 mm), and the dorsum of trunk and tail remain unpigmented until late in postflexion stage when melanophores form on the bases of the second dorsal fin-rays 6–9 (by 12.5–15.5 mm). During transformation a total of eight pigment saddles form below the dorsal fins and on the caudal peduncle (Figure 3B, C).

Minute melanophores are present on the isthmus by the end of the preflexion stage and increase in number during postflexion stage. Ventral midline pigment is always present, extending from near the cleithral symphysis to near the notochord tip (Figures 2, 3). During the postflexion stage a row of melanophores forms along each side of the anal fin (by 9.2 mm) and a single row continues posteriorly from the end of the anal fin to the caudal fin. There are one to three melanophores ventrally and dorsally at the notochord tip in the preflexion stage; the

Table I: Morphometric data of Normanichthys crockeri larvae from Independencia Bight, Peru (range and mean values). Data on adult specimens obtained from the Marine Vertebrate Collection of SCRIPPS (SIO 83–147)

	Preflexion (1.9–6.2 mm)		Flexion (7.1–11.0 mm)		Postflexion (12.5–15.5 mm)		Transformation (20.5–21.6 mm)		Adults (59.3–71.8 mm)	
Morphometric data	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Sn-A/BL	0.37–0.41	0.40	0.39–0.49	0.45	0.46–0.56	0.52	0.49–0.55	0.53	0.58–0.60	0.59
BD/BL	0.11–0.14	0.13	0.15–0.17	0.16	0.17–0.19	0.18	0.18–0.19	0.19	0.16–0.18	0.17
HL/BL	0.12–0.23	0.17	0.21–0.29	0.25	0.26–0.34	0.31	0.33–0.35	0.34	0.34–0.36	0.35
HW/HL	0.37–0.82	0.60	054–0.72	0.59	0.32–0.51	0.46	0.29–0.41	0.38	0.35–0.42	0.38
SnL/HL	0.18–0.36	0.23	0.20–0.28	0.24	0.22–0.31	0.24	0.24–0.24	0.24	0.20–0.23	0.22
ED/HL	0.28–0.54	0.38	0.24–0.29	0.27	0.19–0.28	0.22	0.18–0.22	0.20	0.23–0.24	0.24
P1L/BL	0.02–0.14	0.07	0.14–0.26	0.20	0.24–0.30	0.29	0.23–0.29	0.26	0.23–0.25	0.24
P2L/BL	–	–	–	–	0.05–0.25	0.20	0.16–0.18	0.17	0.16–0.18	0.17

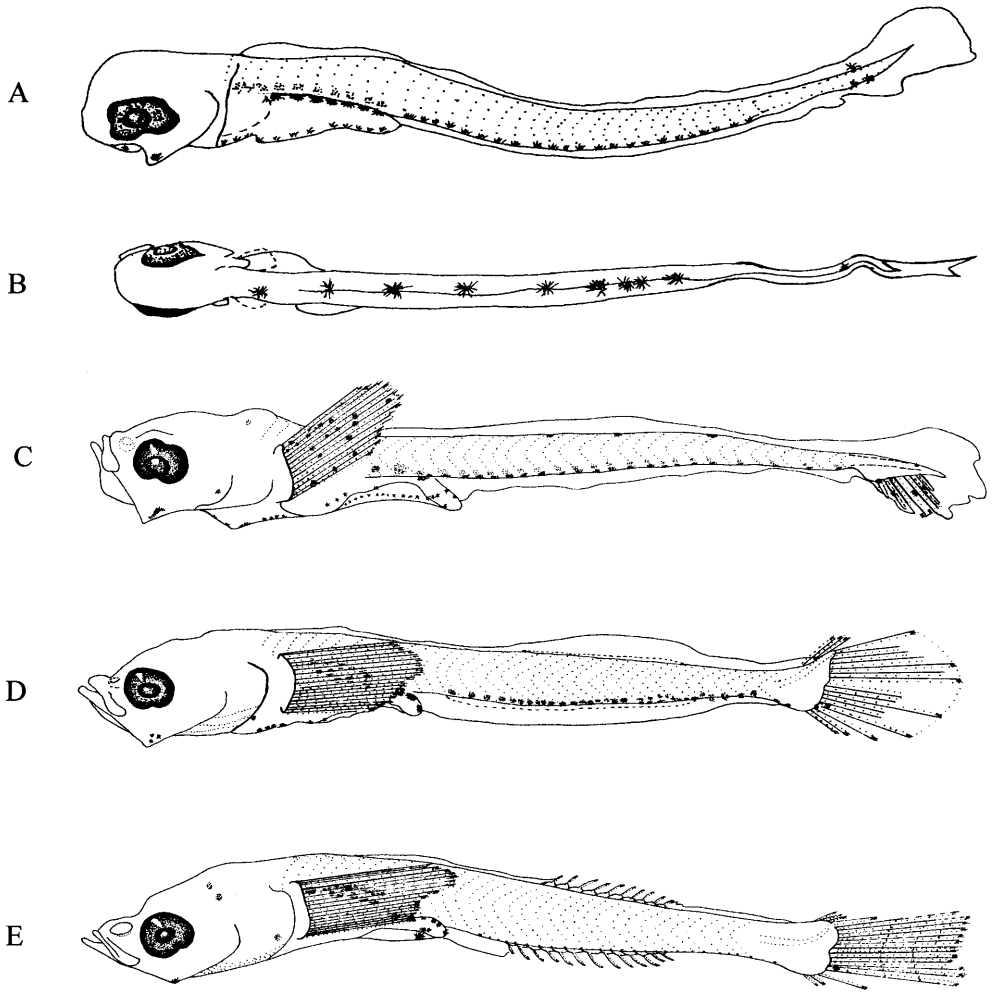

Fig. 2. Larvae of *Normanichthys crockeri*. (**A**) and (**B**) 2.7 mm (early preflexion stage, lateral and dorsal views, respectively); (**C**) 4.9 mm (middle preflexion stage); (**D**) 7.7 mm (flexion stage); and (**E**) 9.2 mm (early postfelxion stage).

dorsal melanophore disappears and ventral melanophores become situated on the lower principal caudal-fin rays during the flexion stage. Preanal finfold pigment present during preflexion, flexion stages, but commonly is not visible in field-collected specimens because the delicate finfold is usually damaged. Ventral pigment in the transformation stage is mostly confined to the base of the anal fin, leaving the lower parts of the body and belly pale (Figure 3B).

Lateral pigment is absent through the postflexion stage. During transformation, eight pigment saddles extend ventrally to just below the lateral line (Figure 3B, C). Six lateral pigment patches between the saddles also extend to just below the lateral line. Dorsal, dorsolateral and mid-lateral pigment patches seem to merge into minutely punctate dots.

Three or four internal pigment patches are located dorsally over the gas bladder and gut, and ventrally on the gut. Dorsal gut pigment becomes embedded at about 7.0 mm. Large, lateral, external melanophores (thre to seven) appear on the abdomen at about 7.2 mm, spread ventrolaterally during the flexion stage (Figure 2D) until about 13.0 mm, then decrease at about 15.7 mm. Ventral gut pigment is present from preflexion to postflexion stages, increases anteriorly until about the mid-postflexion stage, and usually is absent by end of stage.

Pectoral-fin pigment is sparse and minute, but present along the fin-rays in all stages. Pigment develops on the bases of anal- and of some segmented dorsal-fin rays during the postflexion stage, as noted above, but pelvic- and first dorsal-fin pigment is absent until transformation. Pigment develops on the caudal-fin margin and caudal

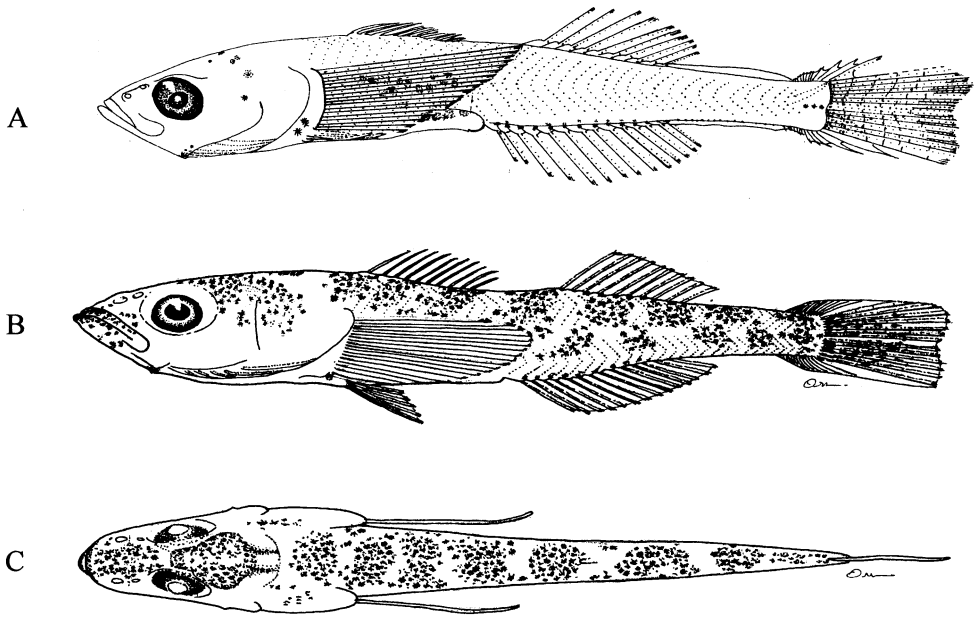

Fig. 3. Larvae of *Normanichthys crockeri*. (**A**) 16.2 mm (late postflexion stage); (**B**) and (**C**) 20.5 mm (transformation stage; lateral and dorsal views, respectively).

peduncle in postflexion stage. A melanophore or two appears on the caudal peduncle at about 11.0 mm (mid-postflexion), increases to three to five melanophores (usually three; Figure 3A). Pigment increases on the bases of the principal caudal-fin rays, usually only on the lower rays until late postflexion stage when it is also found on the upper rays (Figure 3A). In transforming larvae, pigment increases noticeably on the bases of the principal caudal-fin rays to form a solid bar, with sparser pigment extending distally, usually confined to the lower rays.

Osteological development

Ossification of the selected skeletal elements is summarized in Table II. Precision is limited by the small number of cleared and stained specimens. Nevertheless, Table II provides a general picture of the sequence of ossification of the selected elements during the larval stage.

Mandibular arch

Ossification of the maxillary and dentary is well underway and the premaxillary is just beginning to ossify in smallest cleared and stained larva (3.2 mm). By 10.3 mm both jaws are well ossified and the first two teeth are visible anteriorly on the lower jaw (one on each dentary). The 14.2 mm specimen had seven teeth on each dentary but lacked teeth on the upper jaw. The transforming specimen (20.3 mm) had 14 teeth on each dentary and 19 on each premaxillary. The articular and angular begin ossifying at ca. 5.0 mm, and approach the adult shape by ca. 6.0 mm.

Suspensorium

Elements of the suspensorium, particularly the palatine series, ossify later. The symplectic begins to ossify around the lower end of the hyomandibulosymplectic cartilage at ca. 5.4 mm, and is mostly ossified (except at its proximal and distal ends) by 10.3 mm. The hyomandibular is entirely cartilaginous at ca. 5.9 mm, but ossification is well underway by 10.3 mm. By 14.2 mm, the foramen for passage of the trigeminofascialis nerve is apparent and the hyomandibular approaches its adult form. By 20.3 mm the foramen is becoming enclosed in a ventrally directed tube. The quadrate begins to ossify by 10.3 mm, but was not well ossified in the largest specimen (transforming, 20.3 mm). The palatine begins to ossify along its lower margin at ca. 10.5 mm, reaching more or less adult shape but remaining only partially ossified by 20.3 mm. The ectopterygoid begins ossifying along its ventral margin by 14.2 mm and both the metapterygoid and entopterygoid start ossifying after 14.2 mm, but before 20.3 mm; all three were only partly ossified in the largest specimen.

Opercular series

The opercle is the first bone in the opercular series to start ossification, by 5.0 mm; by 10.5 mm it is well ossified. The subopercle and interopercle apparently begin forming

Table II: Sequence of ossification in larvae of Normanichthys crockeri. The initial ossification of an element is indicated by the black point. The arrow indicates the larval size at which the element achieves the general shape it will have in the juvenile and adult. When a bone is still not complete in the 20.3 mm specimen, no arrowhead is drawn on the line

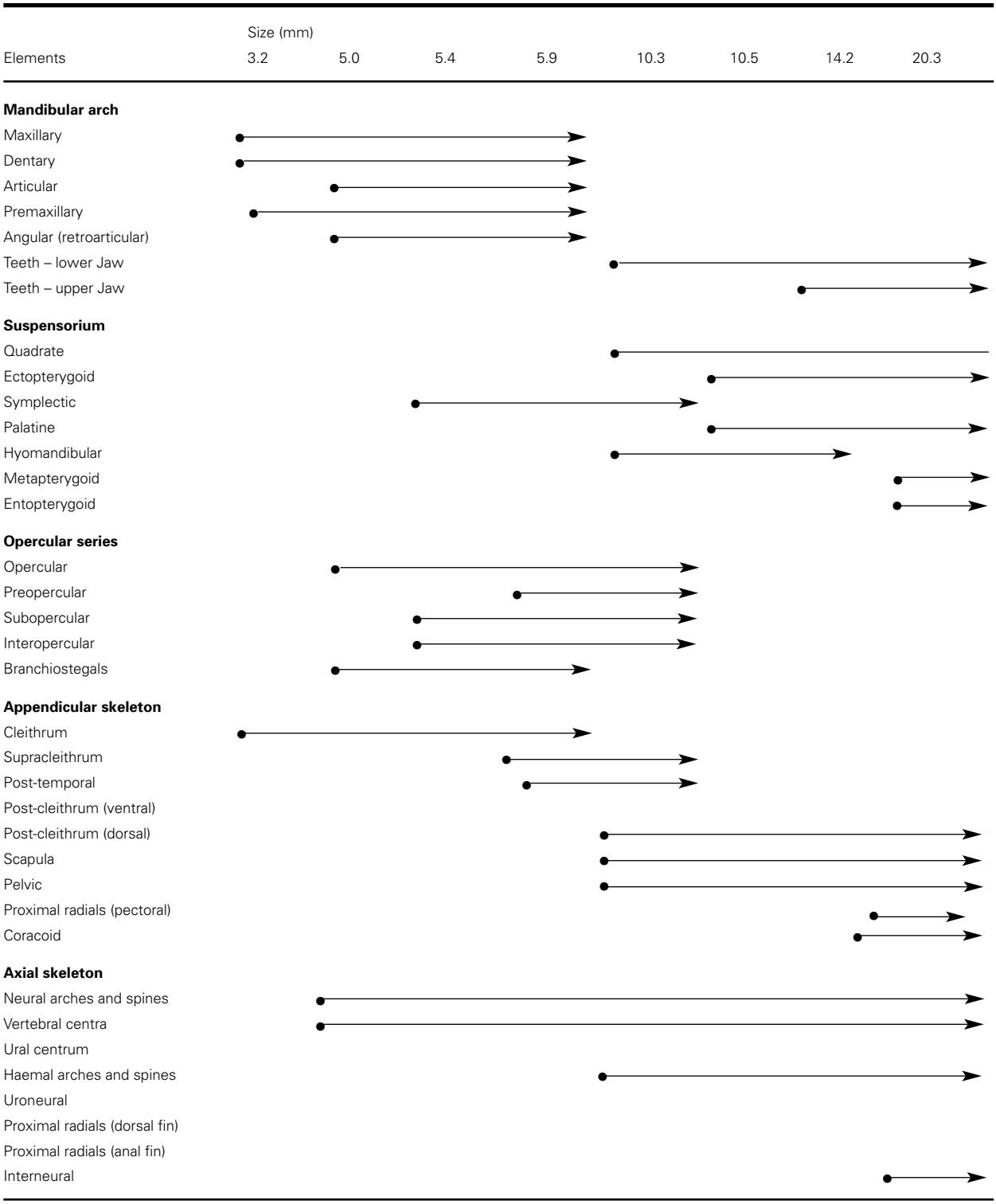

Table II: Continued

Elements	Size (mm) 3.2	5.0	5.4	5.9	10.3	10.5	14.2	20.3
Caudal skeleton								
Parhypural								
Hypural 1+2 (fussed)								
Hypural 3								
Hypural 4								
Hypural 5								
Epural (3)								

simultaneously at ca. 5.4 mm. Both bones approach their adult shapes by ca. 10.3 mm. The last opercular series bone to begin ossifying is the preopercle, at 5.9 mm. Opercular series bones do not develop spines.

Appendicular skeleton

The cleithrum was slender and ossified in the smallest specimen examined (3.2 mm). The supracleithrum begins to ossify by 5.9 mm and the posttemporal starts after 5.9 mm but before 10.3 mm. Both were well ossified with more or less adult form in the 10.3 mm specimen. A small dorsal postcleithrum begins to ossify at ca. 10.3 mm and is well ossified by 20.3 mm. The ventral postcleithrum apparently does not form during the larval stage. The scapula was ossifying in its central region in the 10.3 mm specimen, but was apparently not ossifying in the 10.5 mm specimen. By 14.2 mm all but the distal third of the scapula is ossifying and by 20.3 mm it is almost completely ossified. Ossification of the coracoid commences at ca. 14.2 mm and is nearly complete by 20.3 mm. The pectoral proximal radials are not ossifying at 14.2 mm, but the 20.3 mm specimen had all four radials ossifying in the centre, with the upper two supported by the scapula and the lower two by the coracoid. Pelvic basipterygia were ossifying near their distal ends in the 10.3 and 14.2 mm specimens, but were apparently not ossifying in the 10.5 mm specimen. By 20.3 mm they are well ossified with essentially adult form.

Axial skeleton

Neural arches are the first bones of the axial skeleton to ossify. The first six neural arches ossify by 5.0 mm, nine arches ossify at 5.4 mm, and the first 33 ossify at 10.3 mm (32 in the 10.5 mm specimen). The arches ossify upward from their bases and addition is caudal. The 14.2 mm specimen had 35 neural arches, the last four ossified only at their bases and the first two lacking neural spines and open dorsally, but the next 25 being closed and bearing ossifying neural spines. In the 20.3 mm specimen all 36 neural arches were closed, well ossified, and each, except the last, bore an ossifying neural spine. The next elements of the axial skeleton to begin ossifying are the vertebral centra. The anterior six centra ossify at 5.4 mm and by 10.3 mm all 36 (including urostyle) are well ossified (only the first 31 centra plus the urostyle in the 10.5 mm specimen). Addition of the centra is apparently caudal, except the urostyle begins to ossify (by 5.9 mm) before the most caudal centra. There are 12–15 abdominal and 22–24 caudal vertebrae (12–13+24 in cleared and stained larvae). Neither haemal arches nor haemal spines are ossified in the 5.9 mm specimen, but in the 10.3 mm specimen all haemal arches and spines are ossifying. First five haemapophyses, at vertebral centra 8–12, are ossifying at 10.3 mm and by 14.2 mm seven are present on centra 7–13. Epipleurals begin to ossify at the end of the larval stage: first nine (of 16) being present on centra 7–13.

Other bones of the head

Although ossification of the neurocranium and the hyoid and branchial arches was not specifically examined, development of a few of these bones was noted. In the neurocranium, the first bones to begin ossifying are parasphenotic, after 3.2 mm but before 5.0 mm, and basioccipital at about 5.4 mm. In the 10.3 mm specimen most bones in the brain case were ossifying. In the branchial arch two pairs of pharyngobranchial teeth (one pair large) are present by 5.0 mm and three pairs (one large) are present by 5.4 mm. In the hyoid arch the first four branchiostegal rays are ossifying by 5.4 mm and the fifth is added by 5.9 mm.

Table III: Development of fin rays of Normanichthys crockeri from Independencia Bight, Peru. Notochord flexion begins at about 6.2 mm and ends at ca. 9.0 mm. Transformation begins at ca. 20.0 mm body length. Specimens 59.3–71.8 mm are adults

Length (mm)	First dorsal	Second dorsal	Anal	Caudal Principal	Procurrent	Pectoral	Pelvic
1.9–2.9	–	–	–	–	–	Bud	–
3.3–3.5	–	–	–	–	–	Beg. rays	–
3.6	–	–	–	–	–	5	–
3.9–4.1	–	–	–	–	–	7–8	–
4.6	–	–	–	Hypurals forming		8–9	–
5.0	–	–	–	2+2	–	10–11	–
5.5–5.8	–	–	–	4–5+5	–	13–14	–
5.9	–	–	–	5+5	–	13–15	–
6.1	–	–	–	6+6	–	18	–
6.2	–	–	–	6+6	–	18	–
7.1	–	–	–	7+6	1+1	18	–
7.3	–	Anlage	Anlage	7+6	3+2	18	–
7.7	–	Anlage	Anlage	7+6	3+3	18	–
7.9–8.1	–	Anlage	Anlage	7+6	0–3+1–3	18	–
8.5	–	8	9–10	7+6	1+1	18	–
9.2–9.4	Anlage	10	13–14	7+6	4+3	17–18	Bud
10.0	V	11	14	7+6	4+4	18	Bud
10.3–10.5	X	11	15	7+6	7–13+8–12	18	Bud
12.5–13.2	X	11	14–15	7+6	12+12	18	I,5
14.3	X	11	13	7+6	12+12	17	I,5
14.7	X	10	14	7+6	12+12	18	I,5
15.2	IX–X	10	13	7+6	13+12	18	I,5
15.5	X	10	14	7+6	12+10	18	I,4
20.1	X	10	14	7+6	13+12	19	I,5
20.5	X	10	14	7+6	13+13	18	I,5
21.6	X	11	14	7+6	13+12	18	I,5
21.7	X	10	13	7+6	14+13	19	I,5
59.3–71.8	X–XI	11	14–15	7+6	12–14+12–13	17–19	I,5

Caudal skeleton

Development of the caudal complex starts at about 4.6 mm (Table III). Cartilaginous parhypural and hypurals 1–4 (hypurals 1 and 2 fused) are observed in the 5.0 mm specimen; by 5.9 mm the lower hypural (1+2) and hypural 3 begin to ossify in their central regions and hypural 4 along the lower edge. Parhypural begins to ossify after 5.9 mm; by 10.3 mm both the parhypural and hypurals 1–4 are fully ossified except at their distal ends. Hypural five begins to ossify between 10.3 and 14.2 mm. The three cartilaginous epurals visible at 10.5 mm and epurals 2 and 3 begin ossifying around their centres by 14.2 mm. All elements of the caudal skeleton are largely ossified by the transformation stage (20.3 mm).

Fin development

The sequence of initial fin-ray development is: pectoral, caudal, second dorsal and anal, first dorsal, pelvic (Table III). Pectoral fins, lacking rays, are present at hatching. Developing pectoral-fin rays first become apparent at 3.3 mm, and the full adult complement of 18 (17–19) rays is present by ca. 6.0 mm. Addition of rays is ventral. Uppermost three rays are supported by scapula, the next three by the first pectoral radial, and four each by radials 2–4.

The caudal fin is the second fin to begin formation. Hypurals first appear at about 4.6 mm and principal caudal-fin rays begin to form at about 5.0 mm (Figure 2C), with the full complement of 7+6 principal rays being present by about 7.0 mm (Figure 2D). Posterior procurrent caudal-fin rays begin to form during the flexion stage (Table III; Figure 2D), are gradually added anteriorly until transformation stage (Figure 3B, C), when the full complement of 12–14+12–13 rays is present (Table III; Figure 3B, C). Dorsally, the posteriormost procurrent ray is partially supported by the fifth hypural and the next ray by the third epural; no other dorsal procurrent rays appear to be directly supported by bony or cartilaginous structures during the larval stage. Ventrally, the posteriormost two procurrent rays are supported by the haemal spine of preural centrum two, the next four by a radial cartilage, and the next two by the haemal spine of preural centrum three. The remaining ventral procurrent rays are apparently not directly supported by bony or cartilaginous structures in larvae. The second dorsal fin and anal fin begin to develop simultaneously about mid-way through flexion stage: anlage of each are first visible by ca. 7.3 mm (e.g. Figure 2D), and between 9.2 and 9.4 mm (early postflexion stage, Figure 2E) full complements of 10–11 segmented dorsal fin-rays and 13–15 segmented anal-fin rays are present (Table III). The middle soft rays apparently form first in each fin, and addition is both cephalad and caudad. Dorsal- and anal-fin pterygiophores supporting the soft rays begin to ossify after the rays have formed, between 10.3 and 14.2 mm. Ossification begins simultaneously on each proximal and distal radial near their junction and is nearly complete by 20.3 mm. The spinous dorsal fin begins to develop early in postflexion stage (ca. 9.2 mm), just after dorsal soft-rays and anal rays are completed. Five anterior spines are present by 10.0 mm and the full complement of X–XI spines is completed between 10.3 and 10.5 mm (Table III). Ossification of the pterygiophores supporting the dorsal spines, and of the four interneurals that precede the dorsal fin, begins some time after 14.2 mm but before 20.3 mm. There are no anal-fin spines. Pelvic fin buds form early in the postflexion stage (by 9.2 mm), directly below the pectoral fins. The full complement of one spine and five rays is present by 12.5 mm (Table III, Figure 3A).

Abundance and distribution

Normanichthys crockeri is a pelagic fish endemic to the coastal waters of the southeast Pacific from Peru and Chile; it is abundant in Independencia Bight. There are no published data on the distribution of larval *N. crockeri*. In our surveys *N. crockeri* accounted for 37.5% of the total fish larvae taken in Independencia Bight during 2000. Larval *N. crockeri* were found at all stations, but were most abundant in the vicinities of Santa Rosa and La Vieja Islands: 80.3% were collected at Santa Rosa, followed by Pampa (8.8%), Panteon (7.7%) and Tunga (3.2%) (Figure 1). Larval *N. crockeri* were found only in the samples collected at 10 m depth, at temperatures ranging from 13.4°C to 17.7°C. Over 78% of the larvae ocurred at mean temperatures of 13.5°C to 14.2°C. Recently hatched larvae were caught throughout the year, but abundances were highest in spring (October–November), and approximately 97.7% of all the larvae were taken during October and November.

DISCUSSION

This description of *Normanichthys crockeri* from recently hatched larvae through to transformation supplements the description by Balbontín and Pérez (Balbontín and Pérez, 1980). Results of the two studies were generally concordant; there appeared to be no significant differences between Peruvian and Chilean specimens. However, we found small differences in the sizes at which larval stages began and ended and in the sizes at which the fins formed, with these events typically occurring at somewhat smaller larval lengths in our specimens (Table IV). There were also some slight differences in the sequence of fin formation, in fin-ray counts, and in fin positions (Table IV). These differences were primarily a result of the larger number of specimens and more complete size series available to us.

Diagnostic features

The distinguishing characters of the larvae are: an elongate, moderately slender body; preanal length about half of body length; large, pigmented pectoral fins; a distinct dorsal midline melanophore series on the trunk and tail, which gradually decreases from as many as 13 melanophores early in the preflexion stage to none by the beginning of the flexion stage; pigment ventrally on the gut and tail, at the angular, on the cleithra, and on the caudal region, it has 7+6 principal caudal-fin rays and 36–37 myomeres.

Early larvae of *N. crockeri* resemble those of some cheilodactylids, and to a lesser extent, some aplodactylids and kyphosids. Many species of the last family have similar pigment patterns in the preflexion stage and similar gut length compared with *N. crockeri*, but far fewer vertebrae (usually 25–27, except *Graus nigra*, a girelline with 34 vertebrae). Larval *G. nigra* are unknown and might be confused with *N. crockeri* because of their similar myomere count and potentially similar pigmentation, but, based on other girelline larvae, they may be more heavily pigmented and probably have smaller pectoral fins than *N. crockeri* (Watson, 1996; Konishi, 1988). Larval

Table IV: Comparison of some characters in larval Normanichthys crockeri emphasizing differences between this study and that of Balbontín and Pérez (Balbontín and Pérez, 1980) study

Character	Present study	Balbontín and Pérez, 1980
Collection location	Independencia Bight, Peru*	Valparaiso Bay, Chile
Number of specimens examined	66	19
Size range (mm)	1.9–21.6	4.6–16.3
Total myomeres	36–37	35–37
Fin developmental sequence	1P, Caudal, 2D&Anal, 1D, 2P	1P, Caudal, 2D, Anal, 2P, 1D
Approximate size (mm) at:		
preflexion	1.9–6.2	4.6–<7.2
flexion	6.2–8.5	7.2–<10.6
postflexion	9.2–≤15.5	≥9.8–16.2
transformation	≥15.5–21.6	–
beginning of hypural formation	4.6	6.0–6.1
First appearance of fin anlage		
first dorsal	9.2	16.3
second dorsal	7.3	8.8–9.4
anal	7.3	8.8–9.4
pelvic	9.2	8.6–8.8
First appearance of fin-rays		
pectoral	3.3–3.6	4.6
first dorsal	10.0	16.3
second dorsal	8.5	>9.4–≤10.6
anal	8.5	>9.4–≤10.6
principal caudal rays	5.0	6.9
procurrent caudal rays	6.1	16.3
pelvic	12.5	–
Completion of fin-rays		
pectoral	6.1	10.6
first dorsal	10.3	–
second dorsal	9.2	10.6
anal	9.2	16.3
principal caudal rays	6.1	10.6
procurrent caudal rays	>15.2	–
pelvic	12.5	–
Position of fins (Myomere)		
first dorsal	4^{th}–13^{th}	–
second dorsal	17^{th}–18^{th}–26^{th}–27th	17^{th}–28^{th}
anal	14^{th}–27^{th}	17^{th}–28^{th}
Total number of fin-rays		
pectoral	18–19	17–19
first dorsal	10	–
second dorsal	10–11	10–12
anal	13–14	13–15
principal caudal	7+6	6+6
procurrent caudal	12–14+12–13	–
pelvic	I,5	–

1P, Pectoral; 1D, first dorsal; 2D, second dorsal; 2P, pelvic.
*Included specimens from Chile (SIO 83–147 and SIO 01–75).

Cheilodactylidae and Aplodactylidae have myomere counts (34–36) similar to *N. crockeri*, and some cheilodactylids are pigmented much like *N. crockeri*. However, the following characters should distinguish the larvae of both families from *N. crockeri*: aplodactylids are more heavily pigmented than *N. crockeri* in the preflexion stage, both aplodactylids and cheilodactylids have pigmented but smaller pectoral fins than *N. crockeri*, and both have a single dorsal fin, in contrast to the two separate fins of *N. crockeri* (B. Watson, personal communication).

Osteology

Aspects of skeletal development are described here for the first time. Since bone formation is a gradual process that continues throughout the life of the fish, selection of the point at which an element achieves an essentially adult form (as shown in Table II) is subjective (Moser, 1972). For the most part skeletal development is much like development in a variety of scorpaeniform and other fish (Moser, 1972; Peters, 1983; Potthoff *et al.*, 1984; Yuschak and Lund, 1984; Watson, 1987). Skeletal configuration in the largest cleared and stained *N. crockeri* was consistent with the description by Yabe and Uyeno (Yabe and Uyeno, 1996). A perhaps somewhat unusual feature in *N. crockeri* development is the formation of neural arches and vertebral centra before the haemal arches. This differs from the apparently usual scorpaeniform sequence in which both neural and haemal arches form before the vertebral centra (Matarese and Marliave, 1982; Washington et al., 1984a; Yuschak and Lund, 1984; Matarese and Vinter, 1985), although a *Normanichthys*-like pattern has been reported in Sebastidae (Moser, 1972). A more striking feature of skeletal development in *N. crockeri* is the sequence of initial ossification of the opercular series bones, with the preopercle commencing ossification last, after the interopercle and subopercle. In contrast, the apparently usual condition in scorpaeniform fish is for the preopercle to begin ossifying before (or in some cases simultaneously with) the subopercular and interopercular bones (Moser, 1972; Kendall and Vinter, 1984; Yuschak and Lund, 1984). This difference, perhaps supported by the difference in axial skeleton ossification, suggests the possibility that *Normanichthys* phylogenetic relationships might be elsewhere than with the Scorpaeniformes.

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Larval development of the Pacific sandperch (*Prolatilus jugularis*) (Pisces: Pinguipedidae) from the Independencia Bight, Pisco, Peru

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Morphological development of larval *Prolatilus jugularis* from Bahia Independencia, Pisco, Peru is described. Two hundred and thirty-two specimens were collected with plankton nets in 2000; a developmental series of 40 individuals (2.5–25.9 mm: recently hatched through transformation) was assembled using morphological features and pigmentation. *Prolatilus jugularis* hatches at approximately 2.5 mm, notochord flexion begins at ~5.7 mm and ends at ~6.9 mm, and transformation begins at an unknown size between 14.2–20.3 mm (probably near 20 mm). Diagnostic features of the larvae include a robust body with large head bearing small preopercular spines that begin to form by late preflexion stage; preanal length just under half of body length early in the preflexion stage increasing to near two-thirds of body length in the postflexion stage; and pigmentation primarily on the snout, opercular region, dorsally on the head and gut, laterally above the hindgut, and on the ventral margin of the tail through early flexion stage. A broad mid-lateral stripe begins to form on the trunk and tail late in the flexion stage and dorsal pigmentation forms on the trunk and tail in the postflexion stage. Pectoral-fin rays are first to begin forming, in mid-preflexion stage, followed by principal caudal-fin rays, then by pelvic-, dorsal- and anal-fin rays which apparently begin to form simultaneously near the end of preflexion stage. The dorsal fin is long and continuous, with III–IV short spines and 27–29 soft rays, the anal fin contains 21–23 rays, the first one or two of which may be spine-like, the pelvic fins, with I spine, 5 rays, are below or slightly in front of the pectorals (18–20 rays), and there are 9+8 principal caudal-fin rays and 36–37 myomeres.

INTRODUCTION

After more than a century of research the general knowledge of ichthyoplankton and its ecology remains limited in some regions of the world's oceans (e.g. Richards, 1985; Kendall et al., 1994); this is especially true for South America. Marine fish diversity is high in Peruvian waters, but the larval stages are poorly known; generally, all the scientific work related to Peruvian ichthyoplankton is limited to species of commercial value.

The family Pinguipedidae, originally described by Günther (1860), has been subject of discussion because its monophyly has not been clearly established and the relationships among its genera are uncertain. Several nominal genera have been included in the family and its generic composition is still uncertain, especially in relation to South American forms (see Rosa & Rosa, 1987, 1997). Pinguipedidae currently is thought to be represented in South America by three endemic genera (*Pinguipes*, *Prolatilus* and *Pseudopercis*) and a single species of *Parapercis*. *Pinguipes* includes two species, one distributed from Rio de Janeiro, Brazil to Argentina (*Pinguipes brasilianus*), the other along the coast of Peru and Chile (*P. chilensis*); the genus *Prolatilus* includes only one species: *Prolatilus jugularis* which occurs on the coast of Peru and Chile; *Pseudopercis* includes two species, one restricted to southern Brazil (*Pseudopercis numida*), and the other found from Rio de Janeiro, Brazil, to Argentina (*P. semifasciata*). *Parapersis dockinski* is only known from the Juan Fernández Islands, Chile (Rosa & Rosa, 1997).

Prolatilus jugularis (Valenciennes, 1833) is a marine fish, endemic to the south-east Pacific along the coast of South America from Huacho, Peru (11°11′S) to Chicloe, Chile (43°43′S 72°50′W). The species reaches ~40 cm in length, inhabits rocky and sandy bottoms and feeds on crustaceans, polychaetes and small fish. It is considered a good quality fish and is commercially exploited (Mann, 1954, cited in Rosa & Rosa, 1997).

Based on rearing of artificially fertilized eggs as well as live eggs collected from the plankton, Fischer (1958) proposed five egg developmental phases for *P. jugularis* and described larval growth from hatching to 4.2 mm. Here we complete the larval description based on our more complete series (2.5–25.9 mm) and larger number (232) of specimens. A description of development from just after hatching through transformation, including new information about morphology and pigmentation is provided. This description will facilitate identification of the species in ichthyoplankton samples.

MATERIALS AND METHODS

A developmental series of 40 *Prolatilus jugularis*, 2.5–25.9 mm, was examined. Larvae were collected during eight months in 2000 in the Independencia Bight, Peru.

Figure 1. Study area, Independencia Bight, Pisco, Peru. Sampling locations indicated by black points.

Fifty-six horizontal tows were made with a 60-cm, non-closing bongo net (0.333-mm and 0.505-mm nitex mesh) towed at 10 m depth, and with a half-metre ring net (0.333-mm mesh), towed at the surface; both nets were equipped with calibrated flowmeters. All tows were taken at speeds of 3 kn for 10 min and samples were preserved in 4% formalin solution immediately after collection at each depth at four stations (Figure 1).

In the laboratory all fish larvae were sorted from the samples, identified to the lowest taxon possible, and stored in 4% formalin. A total of 232 larval *P. jugularis* (2.5–25.9 mm body length) was identified, and 40 were selected for description. Three larvae (15.2–25.9 mm, USNM 176428) and four adults (91.2 to 146.0 mm, USNM 176428, 211417) were obtained from the Smithsonian Institution, the National Museum of Natural History; these specimens originally were collected from Chile and Peru.

Larvae were identified by the series method (e.g. Leis & Carson-Ewart, 2000). The series was united on the basis of consistent morphological characters and pigment patterns throughout.

Only specimens in good condition were used and measured (nearest 0.02 mm) with the ocular micrometer of a dissecting microscope within 18 months after collection. Methods of counting and landmarks for measurements are defined by Moser (1996) and Leis & Carson-Ewart (2000). Body parts measured were: body length (BL), snout–anus length (Sn-A), body depth (BD), head length (HL), head width (HW), snout length (SnL), eye diameter (ED), pectoral fin length (P_1L) and pelvic fin length (P_2L). Larval lengths in the following description always refer to BL. Most larvae were lightly stained with alizarin red-S to aid in counting fin rays and in determining the sequence of fin formation. Seven specimens ranging from transformation to adult were selected for radiography in order to obtain more accurate meristic counts. The morphometric series also served as the basis for descriptions of the pigment pattern. Descriptions of pigmentation refer solely to melanistic pigment. Six specimens were illustrated to show pigmentation characters and morphological changes, and to provide identification of all post-hatching developmental stages of *P. jugularis*.

RESULTS

Distribution and abundance

There are no published data on the distribution of larval *Prolatilus jugularis*. In our surveys *P. jugularis* accounted for 1.5% of the total fish larvae taken in Independencia Bight during 2000. Larval *P. jugularis* were found at all stations, but were most abundant at Santa Rosa (38.6%) and Tunga (31.2%), followed by Panteon (23%), and Pampa (7.2%) (Figure 1). Larvae were found only in the samples collected at 10 m depth, at temperatures ranging from 13.4°C to 17.7°C. Over 90% of the larvae occurred at mean temperatures of 13.4–14.2°C. Recently hatched larvae were caught throughout the year (except in May), but in January, February and March the abundances were low and larvae were found at just one of the four stations. Abundances were highest in spring (September–November), with approximately 90.7% of the larvae taken during October and November. Thus spawning extends from at least spring through summer, probably with peak spawning from September to November.

Morphology

Prolatilus jugularis hatches at a small size: our smallest larva (2.5 mm) had a small yolk sac. Notochord flexion begins at ~5.7 mm and ends at ~6.9 mm, and transformation begins at an unknown size between 14.2–20.3 mm (probably near 20 mm). Larval development is a gradual process with no marked changes in body proportions. Larvae are moderately deep-bodied and compressed (juveniles and adults remain compressed but are more elongate). Body depth averages 25% BL in preflexion larvae, increasing to 27% and 29% in flexion and postflexion stages, and decreasing to 21% and 20% in transformation stage and adults, respectively. The gut is coiled and compact early; preanal length increases from near half (47–58%) to about two-thirds BL (64–67%) during larval development, decreasing to 55% in transformation stage and to 47% in adults (Table 1). The head is relatively large, broad, and deeper than the body, with a slight dorsal bulge early in the preflexion stage. Head length averages 31–40% BL through most of the larval period, 36% during transformation stage, and decreases to 32% in adults. Head width increases from 54% to 66% HL in early larvae and decreases to 46% and 39% HL in transforming larvae and adults, respectively. Eye diameter in preflexion stage larva is about 32% HL but decreases to 29% in flexion stage, to 26–27% in postflexion and transformation stages, and to 25% HL in adults. Pectoral fin length rapidly increases from 10% BL in the preflexion stage to 25% in the transformation stage. The pelvic fin length increases from 5% BL late in the preflexion stage to 25% in transformation stage (Table 1).

Table 1. *Morphometric data of* Prolatilus jugularis *larvae from Independencia Bight, Peru (range and mean in decimal fractions).*

Morphometric data	Preflexion (2.5–5.6 mm)		Flexion (5.7–6.9 mm)		Postflexion (7.0–10.6 mm)		Transformation (>10.6–25.9 mm)		Adults (91.2–146.0 mm)	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Sn-A/BL	0.47–0.58	0.54	0.51–0.58	0.55	0.64–0.67	0.66	0.53–0.59	0.55	0.44–0.48	0.47
BD/BL	0.20–0.28	0.25	0.24–0.30	0.27	0.27–0.30	0.29	0.21–0.22	0.21	0.18–0.22	0.20
HL/BL	0.21–0.37	0.31	0.32–0.42	0.36	0.38–0.42	0.40	0.33–0.39	0.36	0.31–0.34	0.32
HW/HL	0.47–0.58	0.54	0.50–0.59	0.55	0.64–0.68	0.66	0.36–0.53	0.46	0.37–0.41	0.39
SnL/HL	0.15–0.36	0.28	0.24–0.29	0.27	0.20–0.29	0.25	0.17–0.22	0.21	0.31–0.33	0.31
ED/HL	0.26–0.37	0.32	0.26–0.35	0.29	0.23–0.30	0.26	0.23–0.33	0.27	0.23–0.27	0.25
P_1L/BL	0.03–0.15	0.10	0.12–0.18	0.15	0.14–0.18	0.16	0.23–0.26	0.25	0.24–0.25	0.24
P_2L/BL	0.0–0.036	0.005	0.013–0.07	0.032	0.20–0.23	0.21	0.24–0.28	0.26	0.23–0.25	0.24

BD, body depth; BL, body length; ED, eye diameter; HL, head length; HW, head width; P_1L, pectoral fin length; P_2L, pelvic fin length; Sn-A, snout–anus length; SnL, snout length.

Relatively well-developed preopercular spination forms during the latter preflexion and flexion stages. This consists of a single row of spines along the posterior preopercular margin, originating as a pair of small spines near the preopercular angle at ~4 mm and increasing to a maximum of 7–10 spines more or less evenly spaced along nearly the full length of the margin by early flexion stage (~6 mm). Small serrations are visible along the margin of the anterior (outer) preopercular shelf in some specimens.

Fin development

The sequence of initial development is: pectoral; caudal and pelvic; dorsal and anal (Table 2). Pectoral fins lacking rays are present in the smallest specimen (2.5 mm). The upper 2–9 pectoral-fin rays develop in the preflexion stage by 4.3 mm and the full adult complement of 20 (18–20) rays is present by late preflexion or early flexion stage (~5.5–5.9 mm). Addition of rays is ventral. The caudal fin begins forming at about 4.5 mm when the hypurals first appear. Principal caudal-fin rays begin to form at about 4.7 mm, with the full complement of 9+8 principal rays present by about 5.7 mm (flexion stage, Figure 2C). The posterior procurrent caudal-fin rays begin to form late in the flexion stage (Table 2) and are gradually added anteriorly through transformation stage, when the full complement of 14–15+11–13 rays is present (Table 2). The pelvic fin buds form early in the preflexion stage (by 4.5 mm) and

Table 2. *Development of fin rays of* Prolatilus jugularis *from Independencia Bight, Peru. Specimens between dashed lines are undergoing notochord flexion. Transformation begins at an unknown size between 14.2–20.3 mm (probably near 20 mm), specimens 91.2–146.0 mm are adults.*

Length (mm)	Preopercular spines	Dorsal	Anal	Caudal		Pectoral	Pelvic
				Principal	Procurrent		
2.5–3.5	1–2	—	—	—	—	—	—
4.3	3	—	—	—	—	9	—
4.5	3	—	—	Hypural form	—	8	Bud
4.7	3	—	—	1+1	—	8	Bud
4.8	3–4	—	—	2+2	—	Damaged	Bud
5.0	5	Anlage	Anlage	3+2	—	13	Bud
5.4	6	Anlage	Anlage	5+5	—	16	Bud
5.5	6–7	Anlage	Anlage	5+5	—	18	Bud
5.6	7	III+19	22	7+6	—	18	4
5.7	8	III+19	20	9+8	—	18	3
5.9	8–9	III+25	22	9+8	—	20	I,5
6.1	9	III+21	21	9+8	—	20	I,5
6.2	9	III+26	21	9+8	—	20	I,5
6.3–6.5	9	III+28	21	9+8	—	19	I,5
6.6	9–10	III+27	21	9+8	—	19	I,5
6.9	10	III+28	21	9+8	1+1	20	I,5
8.4	11	III+29	21	9+8	3+2	18	I,5
10.6	11–12	III+29	23	9+8	5+4	20	I,5
15.2	11	III+29	23	9+8	6+5	20	I,5
20.3	13	III+28	22	9+8	12+9	20	I,5
22.5	12	IV+28	22	9+8	12+10	20	I,5
25.9	16	IV+28	23	9+8	14+12	20	I,5
91.2–146.0	13–16	III–IV+28	22–23	9+8	14–15+11–13	20	I5

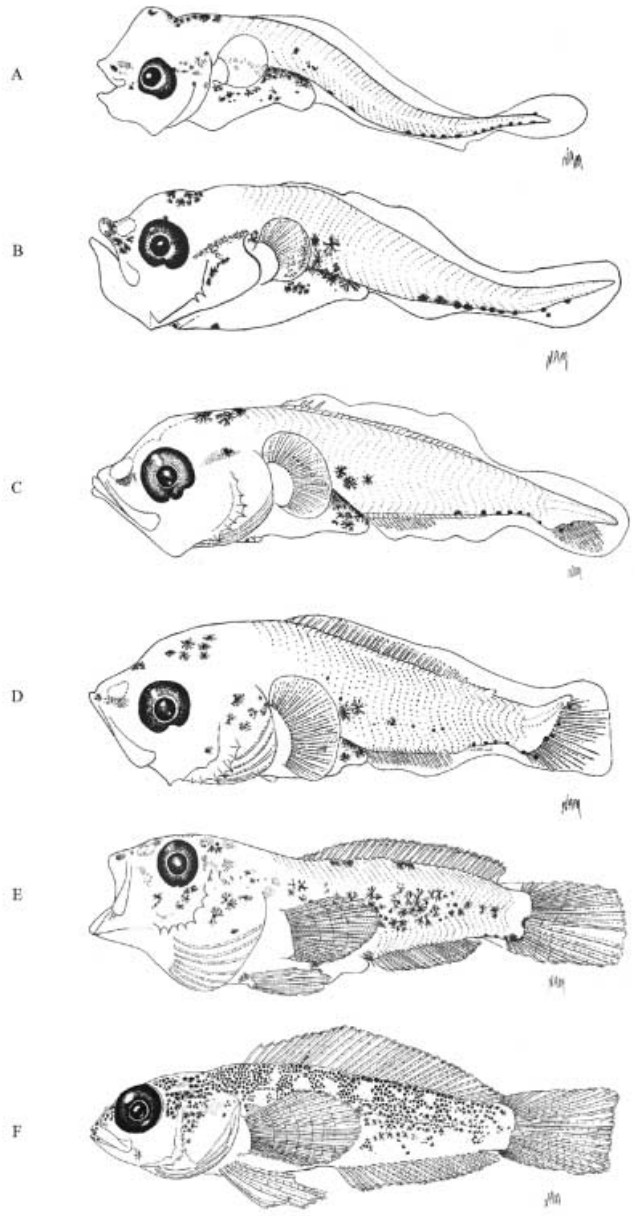

Figure 2. Larvae of *Prolatilus jugularis*. (A) 2.8 mm (early preflexion); (B) 4.3 mm (mid-preflexion); (C) 6.2 mm (late-preflexion); (D) 6.5 mm (mid-flexion); (E) 10.6 mm (late post-flexion); (F) 20.3 mm (transforming). Specimens C and D were slightly less developed than others of similar size.

the full complement of 1 spine and 5 rays is present in the flexion stage by 5.9 mm (Table 2). The dorsal and anal fins begin to develop simultaneously late in the preflexion stage: the anlage of each is first visible by ~5.0 mm, and by mid-flexion stage (6.3–6.5 mm) the full complement of III–IV+27–29 dorsal-fin rays is present (Table 2). Full complements may be present as early as 6.3–6.5 mm and 5.9 mm, but clearly are not present yet in either fin in the 6.2 and 6.5 mm specimens illustrated in Figure 2.

Pigmentation

Melanophores are restricted to the head, gut, trunk and ventral margin of the tail through most of larval development (Figure 2).

Table 3. *Summary of some characters in larval* Prolatilus jugularis *emphasizing progress made in this study since that of Fischer (1958).*

Character	This study	Fischer (1958)
Collection location	Independencia Bight, Peru	Valparaiso, Chile
Number of specimens collected	232	Not specified
Number of specimens examined	40	Not specified
Size range (mm)	2.5–25.9	Eggs to 4.2
Total myomeres	36–37	—
Fin developmental sequence	1P, Caudal, 2P, D and A	—
Approximate size (mm) at:		
Hatching	<2.5	1.9 (2.4–3.1 reared larva)
Preflexion	2.5–5.6	—
Flexion	5.7–6.9	—
Postflexion	>6.9–10.6	—
Transformation	>10.6–25.9	—
Beginning of hypural formation	4.5	—
First appearance of fin anlage		
Dorsal	5.0	—
Anal	5.0	—
Pelvic	4.5 (Bud)	—
First appearance of fin-rays		
Pectoral	>3.5<4.3	3.9
Dorsal	5.6	—
Anal	5.6	—
Principal caudal rays	4.7	—
Procurrent caudal rays	6.9	—
Pelvic	5.6	—
Completion of fin-rays		
Pectoral	5.9	—
Dorsal	6.3–6.5	—
Anal	5.6–10.6	—
Principal caudal rays	5.7	—
Procurrent caudal rays	>22.5	—
Pelvic	>6.5	—
Position of fins (myomere)		
Dorsal	3rd–33rd	—
Anal	12th–31st	—
Total number of fin-rays		
Pectoral	20	—
Dorsal	III–IV+28	—
Anal	22–23	—
Principal caudal	9+8	—
Procurrent caudal	14–15+11–13	—
Pelvic	I,5	—

A, anal; C, caudal; D, dorsal; 1P, pectoral; 2P, pelvic.

Head region

Head pigment always is present. Our smallest larva (2.5 mm) had eight stellate melanophores scattered dorsally above the brain, scattered melanophores (external and internal) laterally on the head, and on the upper jaw and snout. In that specimen the eyes were becoming pigmented. By 2.8 mm the dorsal pigment on the head increases (11 melanophores), the eyes are fully pigmented, and the pigment on the snout and upper jaw increase noticeably (Figure 2A).

In the remaining preflexion stage and flexion stage uniform pigmentation gradually develops over the midbrain region, with 11–24 (usually 11–13) darker melanophores scattered on top (by 6.9 mm). At the same time pigmentation spreads anteriorly over the forebrain and posteriorly onto the nape and anterior few myomeres: for example a 4.7 mm specimen had 2 melanophores on the nape and 3 on the trunk, while 5.4 and 5.6 mm specimens had 3 and 2 at the nape and 5 and 2 on the trunk, respectively. Melanophores at the nape usually are internal. Some dorsal melanophores on the head begin to extend internally during mid-preflexion stage (>4.7 mm); there usually are 1–4 internal melanophores. Both internal and external pigment is present laterally on the head throughout larval development (Figure 2). In 2.5–10.6 mm specimens, this pigment is posterior to the eye and extends from the level of the midbrain to just anterior to the pectoral fin; there are 1–8 external melanophores during the preflexion stage, increasing noticeably during notochord flexion. There are 1–2 melanophores on the interior and exterior surfaces of each nasal capsule throughout development. In specimens up to 6.2 mm, 2–6 melanophores (internal and external) were observed between the eyes. Pigment increases dorsally and dorsolaterally on the head, so that by transformation stage (~20.3 mm) the upper half of the head is heavily pigmented while the lower half remains very lightly pigmented (Figure 2F).

There are 1–2 and 5–12 melanophores on the interior and exterior surfaces of the upper jaw, respectively; in postflexion specimens these are on the central part of the jaw (Figure 2E). The lower jaw is unpigmented before transformation (Figure 2F). One to three (usually 1) ventral melanophores are found in the gular region through postflexion stage, but disappear at transformation.

Gut, trunk and tail regions

The gut is always pigmented dorsally and anteriorly, with densest pigmentation internally over the dorsal and dorsolateral surfaces of the swim bladder and nearly the full length of the gut. During the preflexion stage (~2.5–5.6 mm, Figure 2A,B) there are many internal and external melanophores (19–31, usually 19–22), primarily internally. Pigment spreads downward over the dorsolateral surfaces of the swimbladder and hindgut during the flexion stage (~5.7–6.9 mm, Figure 2B,C), extending to near the anus posteriorly. At the end of the flexion stage and during the postflexion stage (~7.0–10.6 mm, Figure 2E) the internal pigment becomes increasingly difficult to see through the thickening abdominal wall.

Ventral pigmentation is absent on the gut through 3.5 mm; from 3.6 mm onward there are 1–5 external melanophores along the ventral margin of the hindgut (usually 1–2 in the preflexion stage; 3–5 in the postflexion stage). The ventral hingut pigmentation is absent in transforming specimens.

External pigment develops dorsally and laterally on the trunk and tail, and on the ventral margin of the tail. The dorsal pigment first forms anteriorly: preflexion- and flexion-stage specimens have 1–6 (usually 1–3) internal melanophores after the nape; during the postflexion stage (Figure 2E) the pigment on this area increases, forming a band with the opercular melanophores.

The lateral surface of the trunk is always pigmented, primarily on the area above the hindgut in larvae smaller than ~6.2 mm (preflexion through mid-flexion, Figure 2A–C); the number of melanophores here increases with larval growth. In specimens larger than 5.4 mm a group of 3–12 melanophores (usually 3–7) in the hindgut area extends from the trunk over the upper side of the gut. Late in the flexion stage (6.6–6.9 mm) 12–14 melanophores begin to form a lateral band on the trunk and tail; this pigmentation increases noticeably (>26 melanophores during the postflexion stage), forming a broad midlateral stripe (Figure 2E). During the transformation stage, nine pigment saddles form and extend ventral to, or just below, the lateral line (Figure 2F). Some pigment patches between the saddles also extend to just below the lateral line.

A single row of melanophores is always present along the ventral midline of the tail from postanal myomere 4–6 nearly to the end of the notochord. The number of melanophores in this series decreases during development, from 8–19 (usually 11–14) early in the preflexion stage to only the posterior 4–5 late in the postflexion stage (Figure 2A–E); there are 0–1 (usually none), on the caudal peduncle when present, in transforming specimens (Figure 2F). It is possible that some of the anterior melanophores in the ventral series migrate upward toward the lateral line. The ventral melanophores on the notochord tip become situated at the bases of some of the principal caudal-fin rays (Figure 2C–E); in transforming specimens pigment increases noticeably on the bases of the principal rays, with sparser pigment extending distally. During the preflexion stage 1–3 melanophores can be found on the caudal finfold near the body margin (Figure 2B). These subsequently become located at or near the base(s) of one or more of the lower caudal-fin rays. Early preflexion specimens have a melanophore dorsally on the notochord tip (Figure 2A), which disappears or becomes internal during the preflexion stage.

DISCUSSION

Fischer (1958), described larval *Prolatilus jugularis* from hatching to 4.2 mm. In our study, complete larval development from recently hatched larvae through transformation is described and illustrated for the first time. In Table 3 we compare some of the results of our study with those of Fischer (1958). The few results that can be compared between the two studies generally are concordant.

Identification

Larval *Prolatilus jugularis* hatch at about 2–3 mm, notochord flexion begins at ~5.7 and ends at ~6.9 mm, and transformation begins at an unknown size between 14.2–20.3 mm (probably near 20 mm). The most important diagnostic features of the larvae include a robust body with large head bearing small preopercular spines that begin to form by late preflexion stage; preanal length just under half of body length early in the preflexion stage increasing to near two-thirds of body length early in the postflexion stage; and pigmentation primarily on the snout, opercular region, dorsally on the head and gut, laterally above the hindgut, and on the ventral margin of

the tail through early flexion stage. A broad mid-lateral stripe begins to form on the trunk and tail late in the flexion stage and dorsal pigmentation forms on the trunk and tail in the postflexion stage. Pectoral-fin rays are first to begin forming, in mid-preflexion stage, followed by principal caudal-fin rays, then by dorsal-, anal-, and pelvic-fin rays which apparently begin to form simultaneously near the end of preflexion stage. Pelvic fins are below or slightly in front of the pectorals, the dorsal fin is long and continuous, with III–IV short spines and 27–29 soft rays, the anal fin is long, with 21–23 rays, first one or two of which may be spine-like, there are I,5 pelvic-fin rays, 9+8 principal caudal-fin rays and 36–37 myomeres.

The early larvae of *P. jugularis* might be difficult to distinguish from those of some other families as their general morphology is similar to that of a number of larvae with relatively large, rounded heads and a row of melanophores midventrally on the tail. This includes some scombrids, nemipterids, sparids, microcanthids, blenniids, nomeids and some myctophids. The nemipterids, sparids, and microcanthids have fewer myomeres than *P. jugularis* (22–24, 24, and 25 myomeres respectively, vs 36–37). Most nomeids have 30–31 or 40 myomeres; the two eastern Pacific species (both *Psenes*) that have myomere counts similar to *Prolatilus jugularis* have preanal length $<50\%$ BL during the preflexion stage, lack preopercular spines, and have moderately large pelvic fins that form early, far sooner than pelvic fins form in *P. jugularis*. Larvae of the other families commonly have myomere counts in the mid- to high 30s. The blenniids typically have a shorter preanal length than *P. jugularis* (usually $\approx 40\%$ BL except $\approx 50\%$ in many Salariinae, vs usually $\geqslant 50\%$ in *P. jugularis*) and commonly have enlarged and/or pigmented pectoral fins, may develop much larger preopercular spines than *P. jugularis*, and may develop relatively large recurved teeth. Preflexion stage larvae of most scombrid species also usually have preanal length $<50\%$ BL ($\approx 50\%$ in *Euthynnus*, $>60\%$ in *Acanthocybium*), and all have a larger mouth, larger preopercular spines (except scomber), larger teeth, and develop a longer snout compared with *P. jugularis*. Myctophids generally have an uncoiled, striated gut, most lack preopercular spines, and they commonly are more lightly pigmented than *P. jugularis*.

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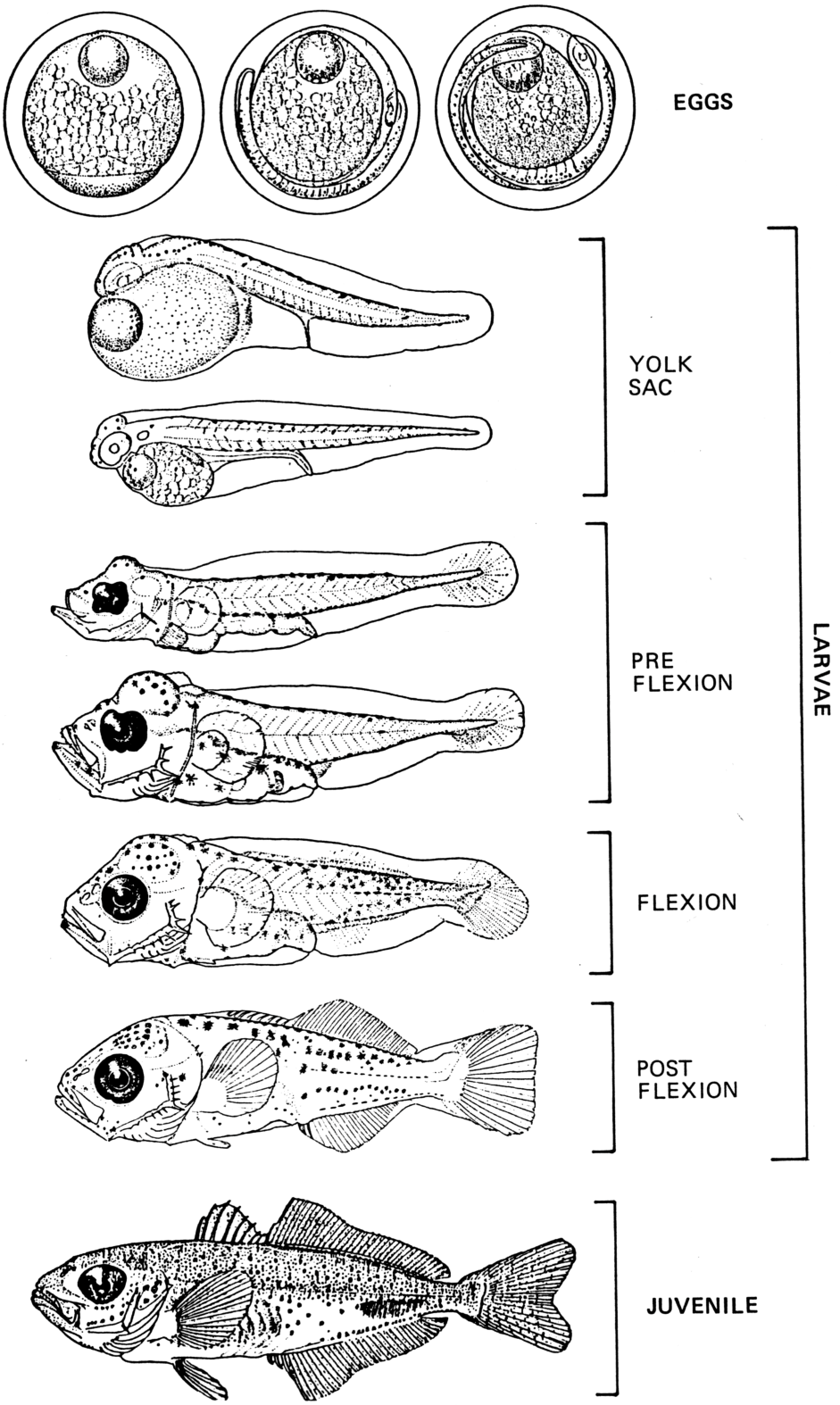
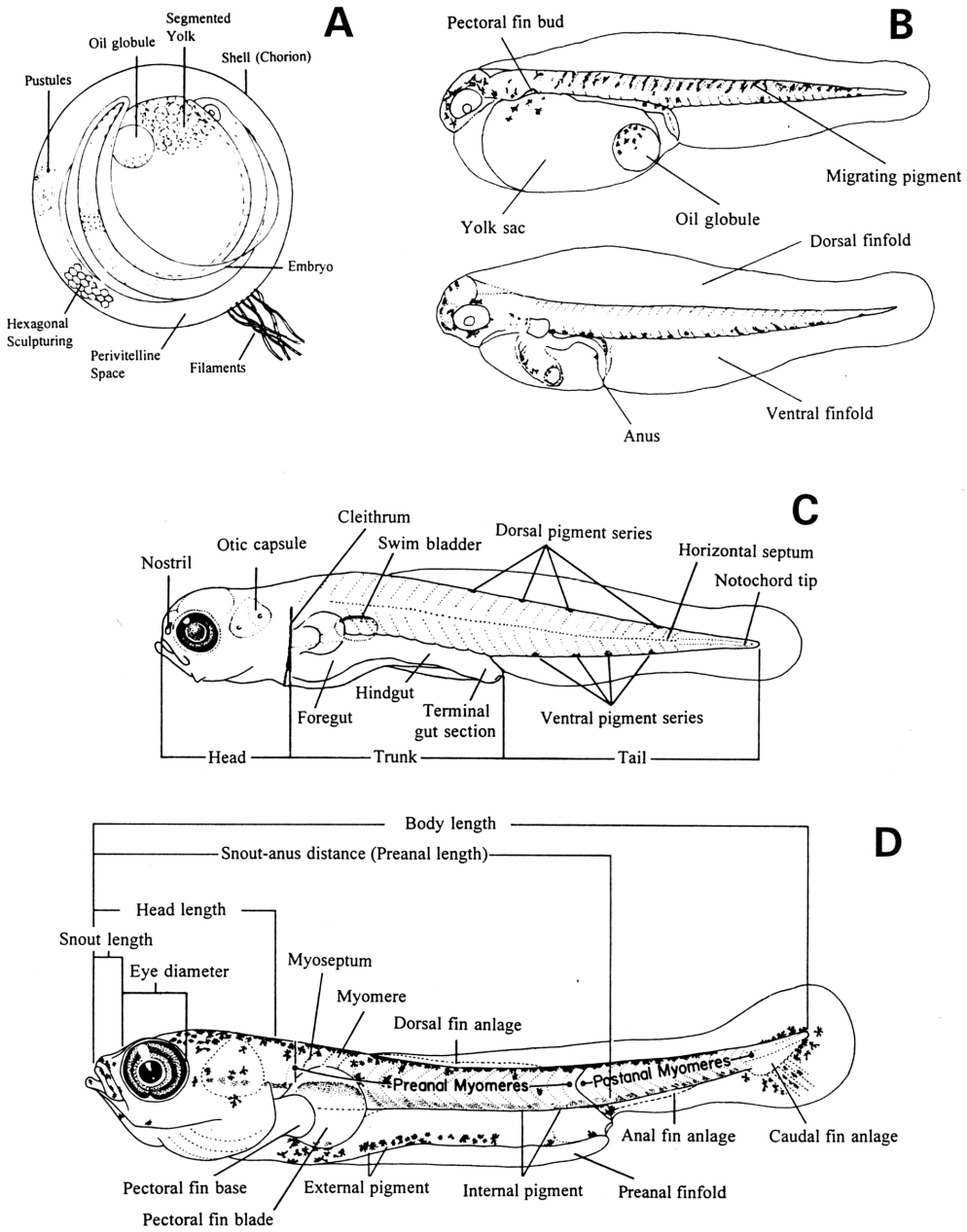
8. APPENDICES

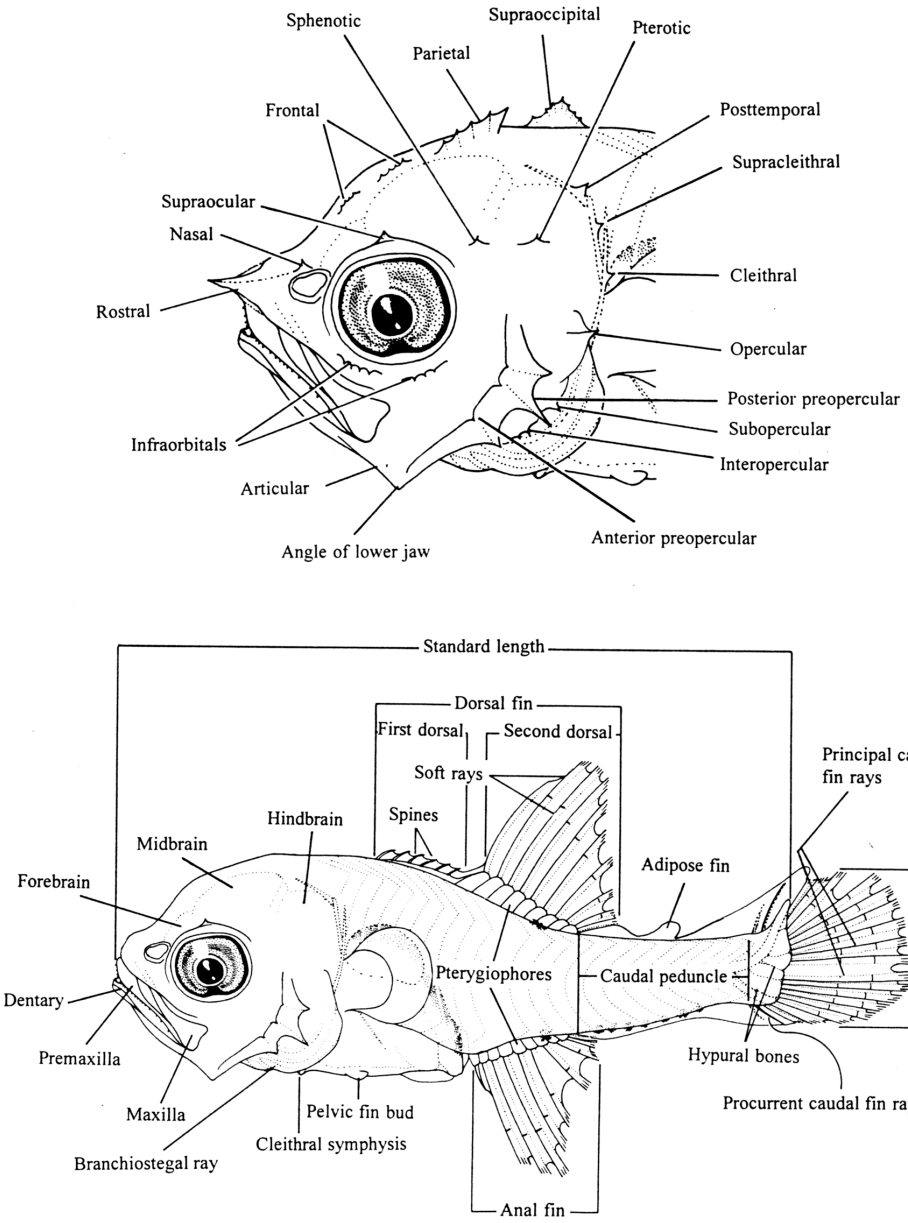
8.1 Appendix 1. Early life history stages of *Trachurus symmetricus* (from Moser et al., 1984).



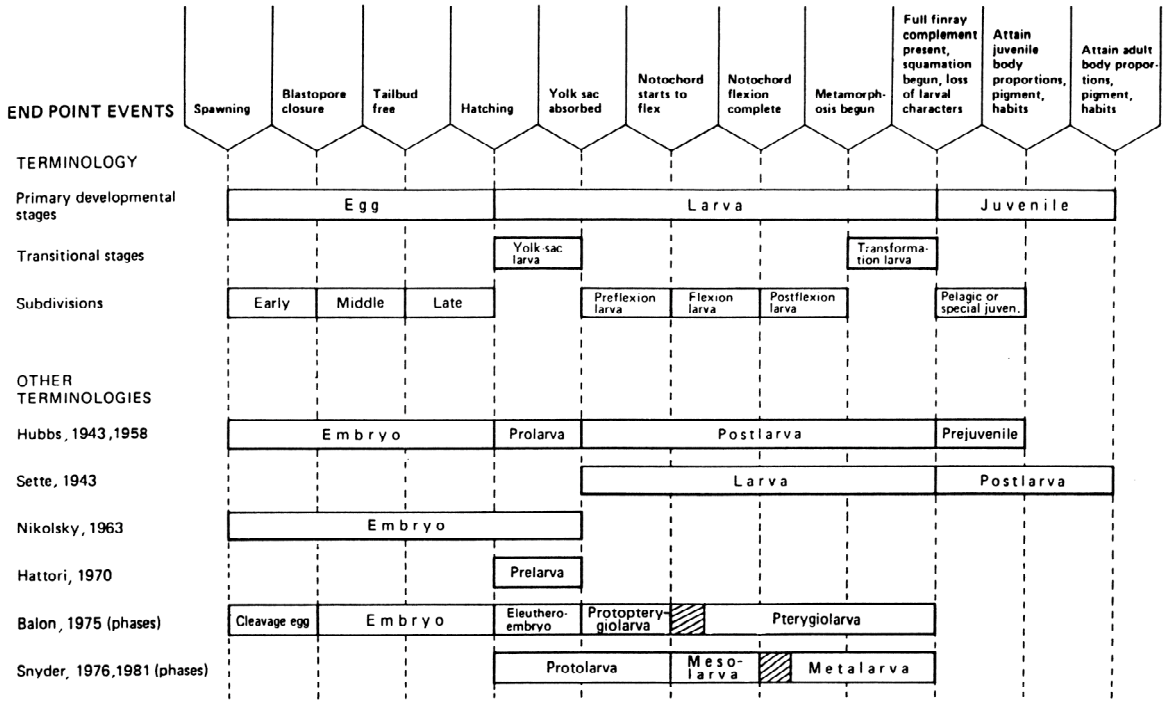
8.2 Appendix 2. Anatomical and morphometric features of the early stages of fishes. (A) Composite illustration of a fish egg. (B) Early and late yolk-sac larvae. (C) Preflexion larva. (D) Late preflexion larva (from Moser et al., 1996).



8.3 Appendix 3. Anatomical and morphometric features of the Postflexion stage of a fish larva. The enlargement (above) shows examples of head spines (from Moser et al., 1996).



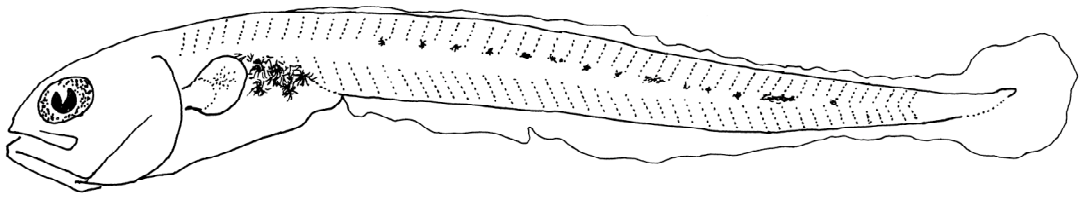
8.4 Appendix 4.Terminology of early life history stages (from Moser et al. 1984).



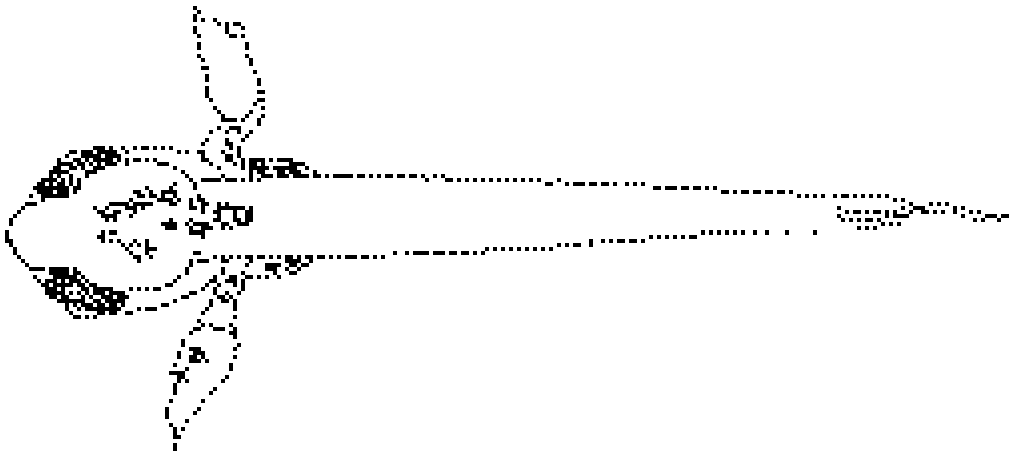
8.5 Appendix 5. Larval descriptions of the Peruvian fishfauna published up today (Guzman & Ayon, *pers. comm.*).

Family	Genus/specie	Reference
Atherinidae	*Odonthestes regia regia*	Ch. de Vildoso & E. Chumán, 1964
Bathylagidae	*Bathylagus nigrigenys*	Sandoval de Castillo, 1979
	Leuroglossus stilbius	Sandoval de Castillo, 1979
Bothidae	*Bothus constellatus*	Guzmán & Ayón, 1995
Bregmacerotidae	*Bregmaceros bathymaster*	Guzmán & Ayón, 1995
Carangidae	*Chloroscombrus orqueta*	Guzmán & Ayón, 1995
	Selene pruvianus	Guzmán & Ayón, 1995
Carangidae	*Trachurus picturatus murphi*	Santander & S. de Castillo, 1971
Coryphaenidae	*Coryphaena hippurus*	Guzmán & Ayón, 1995
Clupeidae	*Sardinops sagax sagax*	Santander & S. de Castillo, 1971
Cynoglossidae	*Symphurus* sp.	Sandoval de Castillo, 1979
Gempylidae	*Gempylus serpens*	Guzmán & Ayón, 1995
Gonostomatidae	*Cyclothone signata*	Guzmán & Ayón, 1995
Engraulididae	*Engraulis ringens*	Einarsson & R. de Mendiola, 1963
Labridae	*Halichoeres* sp.	Guzmán & Ayón, 1995
Merlucciidae	*Merluccius gayi peruanus*	Santander & S. de castillo, 1969
Myctophidae	*Diogenichthys laternatus*	Sandoval de Castillo, 1979
	Gonichthys tenuiculum	Sandoval de Castillo, 1979
	Myctophum nitidulum	Sandoval de Castillo, 1979
	Triphoturus mexicanus	Sandoval de Castillo, 1979
	Benthosema panamense	Guzmán & Ayón, 1995
	Lampanyctus sp.	Guzmán & Ayón, 1995
	Triphoturus sp.	Guzmán & Ayón, 1995
Nomeidae	*Cubiceps pauciradiatus*	
	Psenes sio	
Paralichthyidae	*Citharichthys* sp.	Sandoval de Castillo, 1979
	Syacium ovale	Guzmán & Ayón, 1995
Polynemidae	*Polydactylus* sp.	Guzmán & Ayón, 1995
Photichthyidae	*Vinciguerria lucetia*	Sandoval de Castillo, 1979
Sciaenidae	*Larimus* sp.	Guzmán & Ayón, 1995
Scombridae	*Auxis* sp.	Sandoval de Castillo, 1979
	Scomber japonicus peruanus	Santander & S. de Castillo, 1972
	Scomberomorus sp.	Guzmán & Ayón, 1995
Soleidae	*Achirus* sp.	Guzmán & Ayón, 1995
Trichiuridae	*Lepidopus* sp.	Sandoval de Castillo, 1979

8.6 Appendix 6. Outline illustrations of representative larvae of fishes presented in the Independencia Bay during this study.

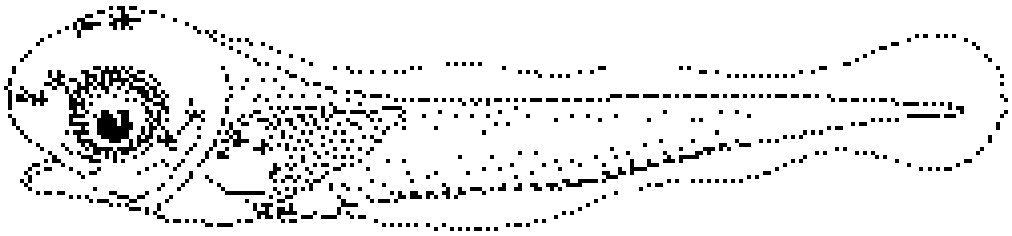


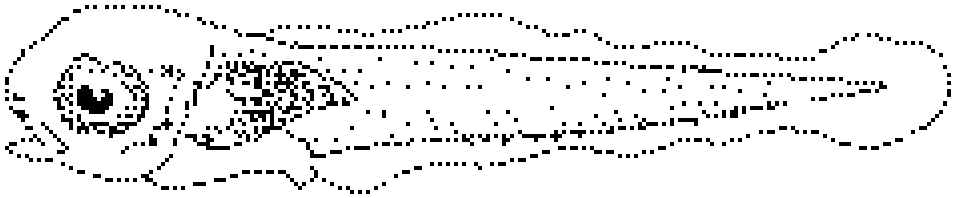
ATHERINIDAE
Odontesthes regia regia (Silversides, Pejerey)
Preflexion

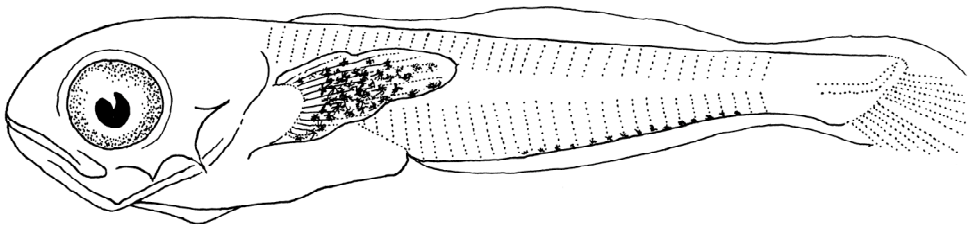


BLENNIIDAE
Hypsoblennius sp. (Blenny, Blénido, Borrachos)
Preflexion

Appendix 6 (continued)

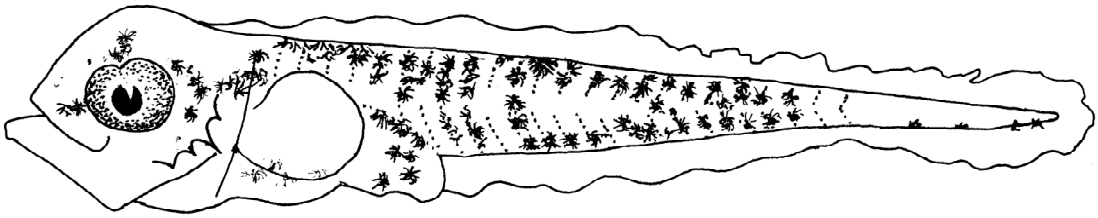




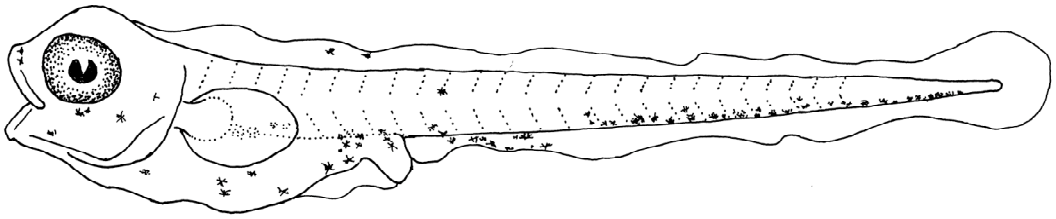


BLENNIIDAE
Hypsoblennius sp. (Blenny, Blénido, Borrachos)
Preflexion

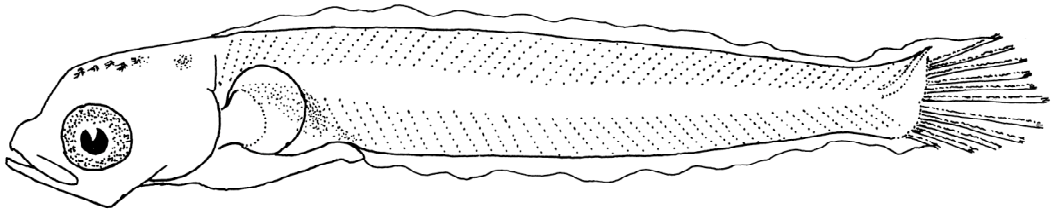
Appendix 6 (continued)



CARANGIDAE
Seriola sp. (Jacks, Fortuna)
Preflexion

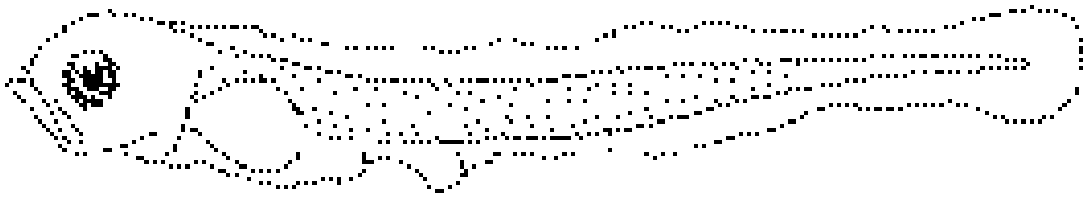


CENTROPOMIDAE
Centropomus (?) (Snooks, Robalos, Constantinos)
Preflexion

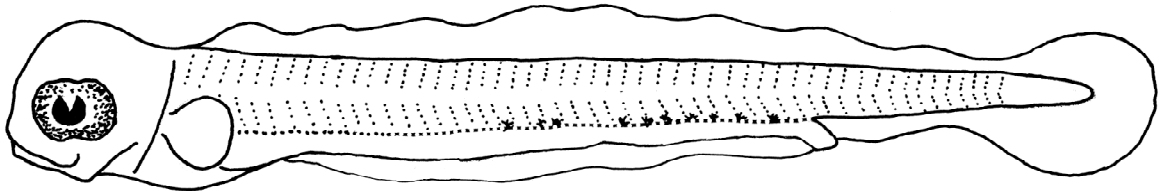


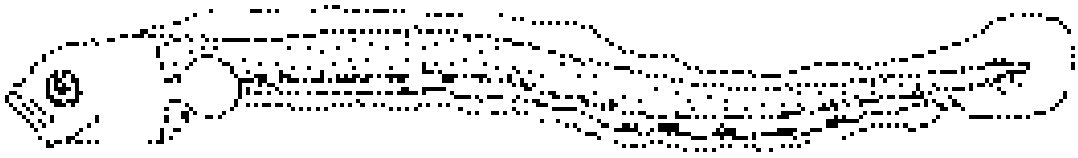
CHAENOPSIDAE
Emblemaria sp. (Tube blennies, Trambollitos)
Postflexion

Appendix 6 (continued)



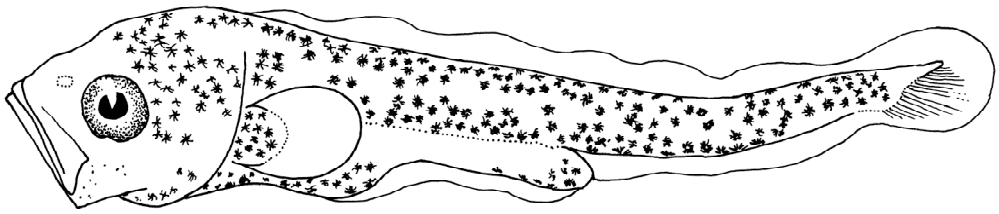
CHEILODACTYLIDAE
Cheilodactylus variegates (Peruvian morwong, Pintadilla, Páramo)
Preflexion



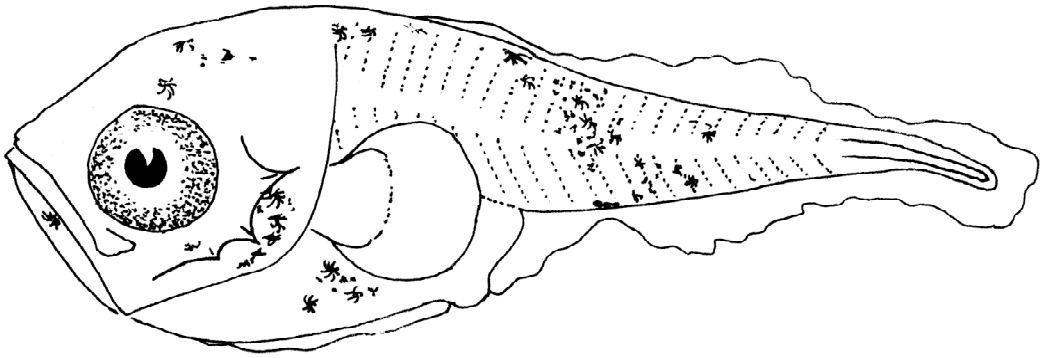


CLUPEIDAE
Sardinops sagax sagax (Pacific sardine, Pilchard, Sardina)
Preflexion

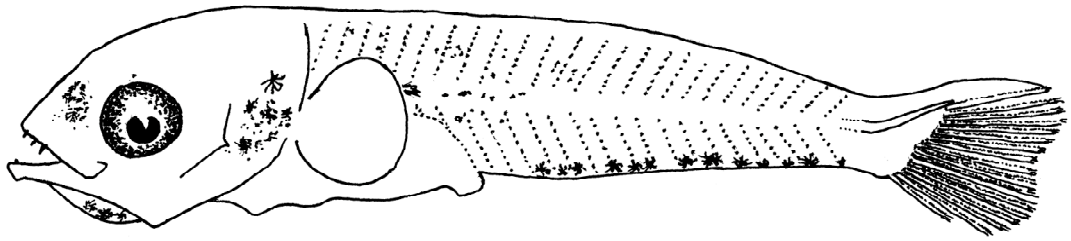
Appendix 4 (continued)



CORYPHAENIDAE
Coryphaena hippurus (Common dolphinfish, Perico, Dorado)
Flexion

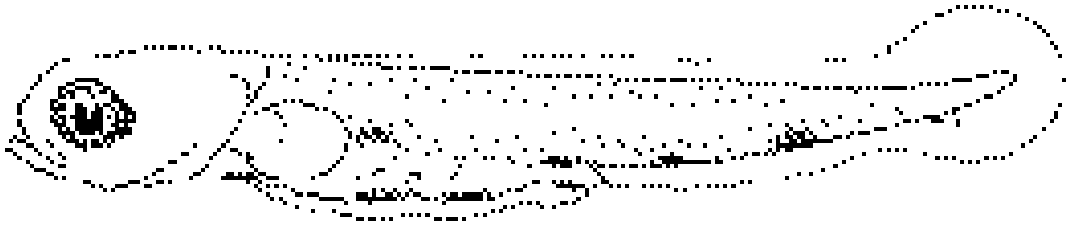


EPHIPPIDAE
Parapsettus (panamensis?) (Spadefishes, Camisetas, Curacas)
Preflexion

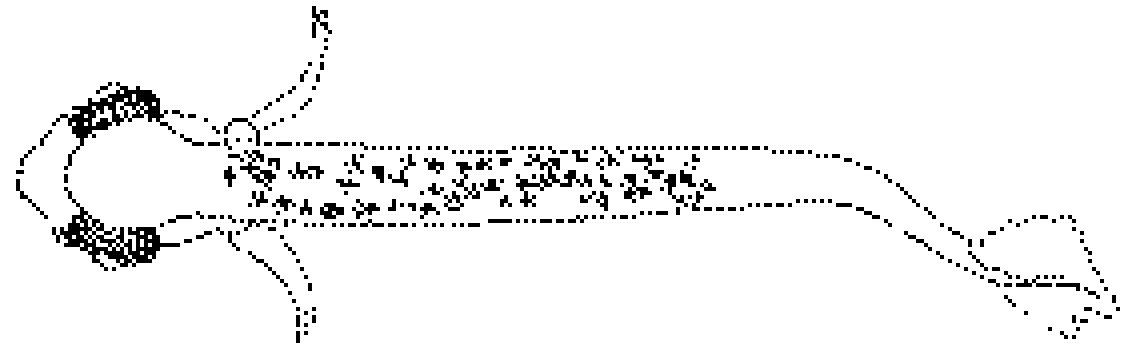


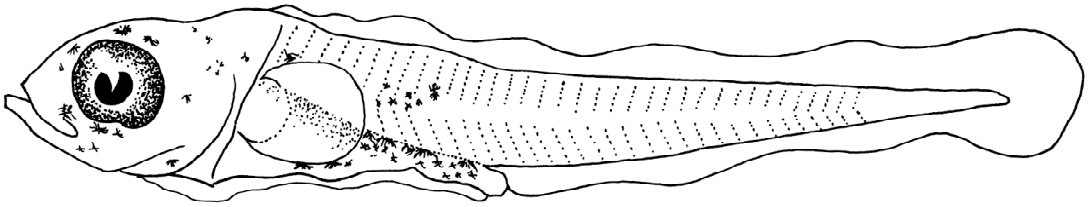
GERREIDAE
Eugerres periche (Mojarras, Mojarra periche, Periche mojarra)
Postflexion

Appendix 6 (continued)



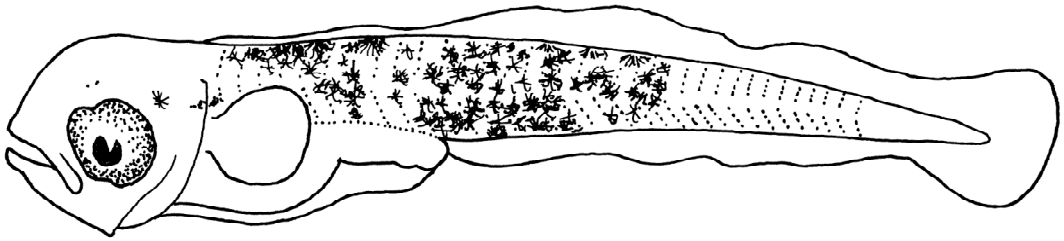
GOBIIDAE
Evermania zosterura (Gobies, Gobios, Gobidos)
Prelexion





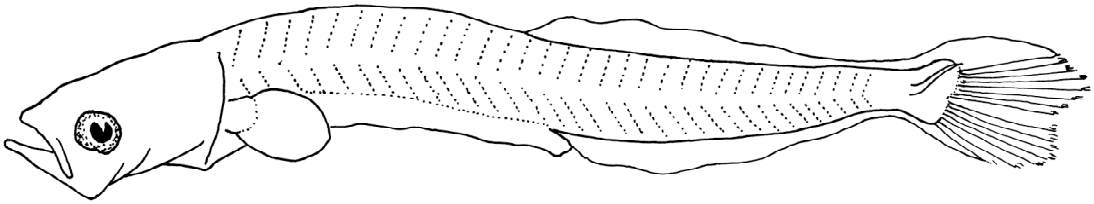
GOBIIDAE
Evermania zosterura (Gobies, Gobios, Gobidos)
Preflexion

Appendix 6 (continued)



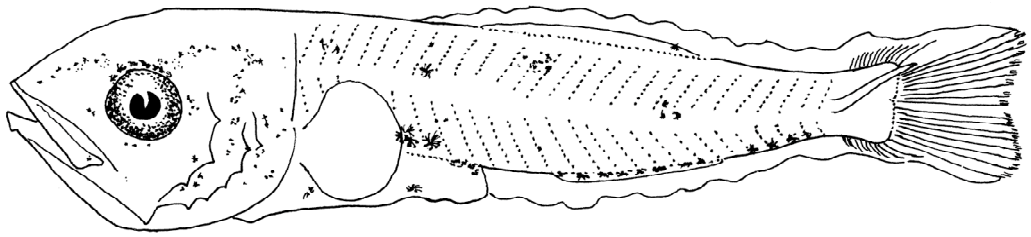
GOBIIDAE
Evermania zosterura (Gobies, Gobios, Gobidos)
Preflexion

GOBIIDAE
Evermania zosterura (Gobies, Gobios, Gobidos)
Preflexion

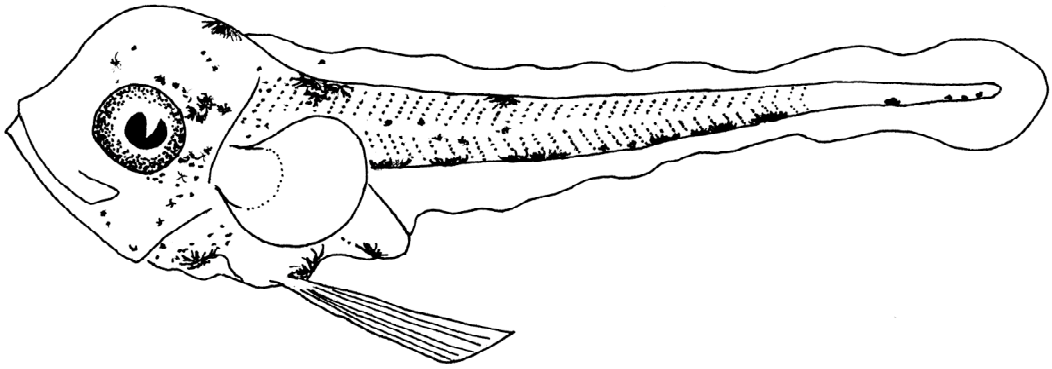


GOBIIDAE
Evermania zosterura (Gobies, Gobios, Gobidos)
Postflexion

Appendix 6 (continued)



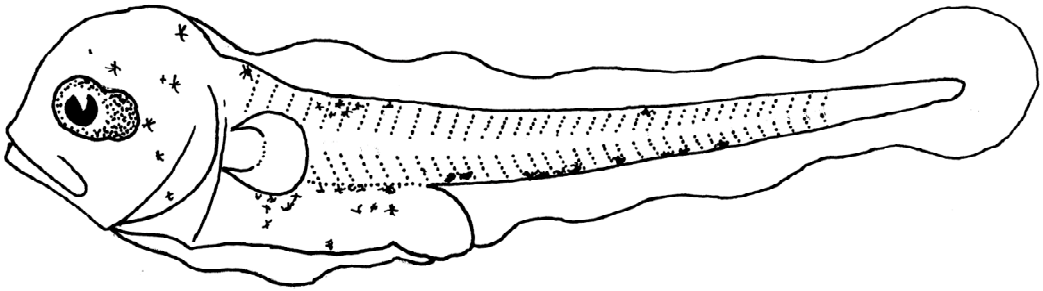
HAEMULIDAE
Anisotremus sp. (Grunts, Chitas, Cabinzas)
Postflexion

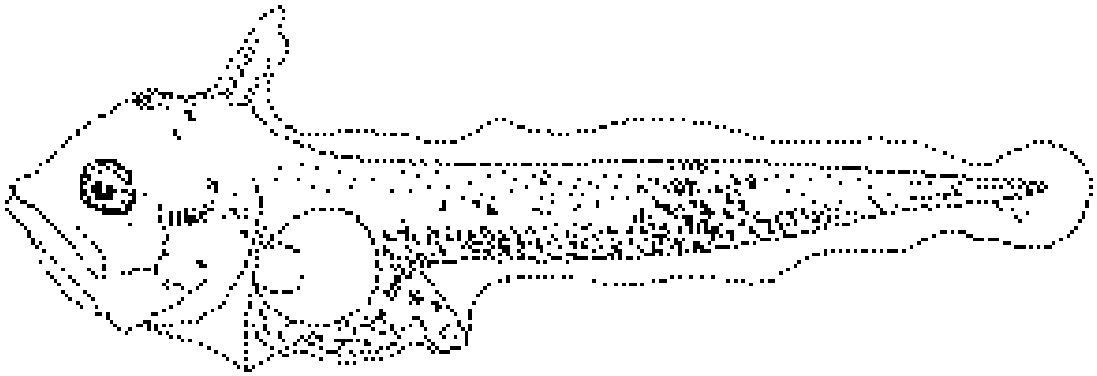


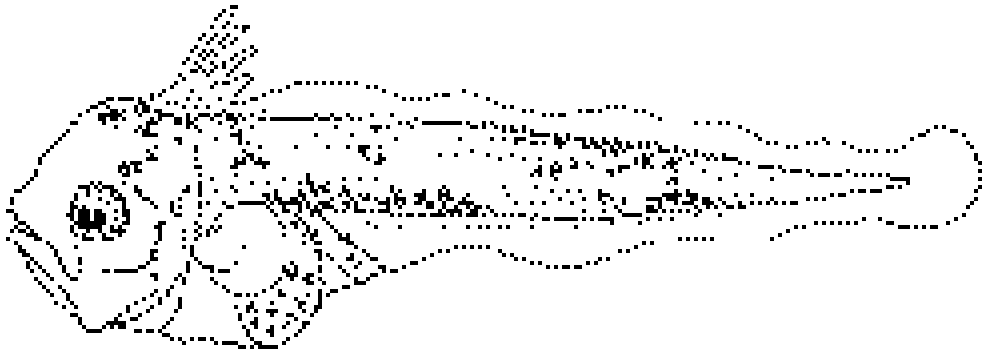
NOMEIDAE
Nomeus gronovii (Man of warfish, Blackrags, Peces Meduza, Pez azul)
Preflexion

SCOMBROIDEI
? (Tunas, Mackerels, Bonitos, Atunes)
Preflexion

Appendix 6 (continued)

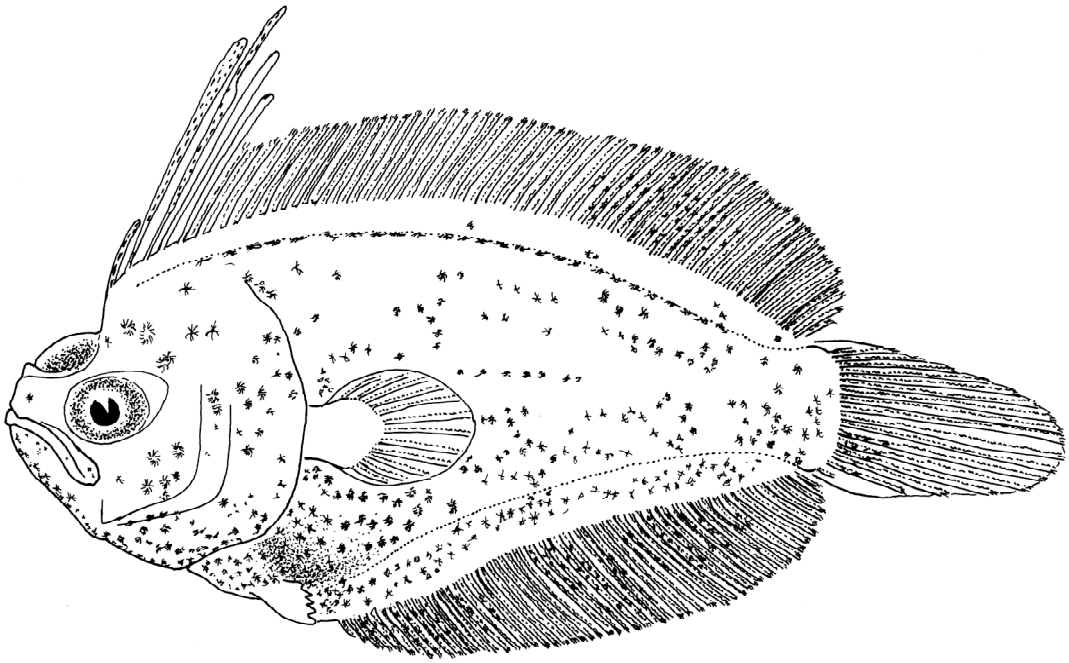




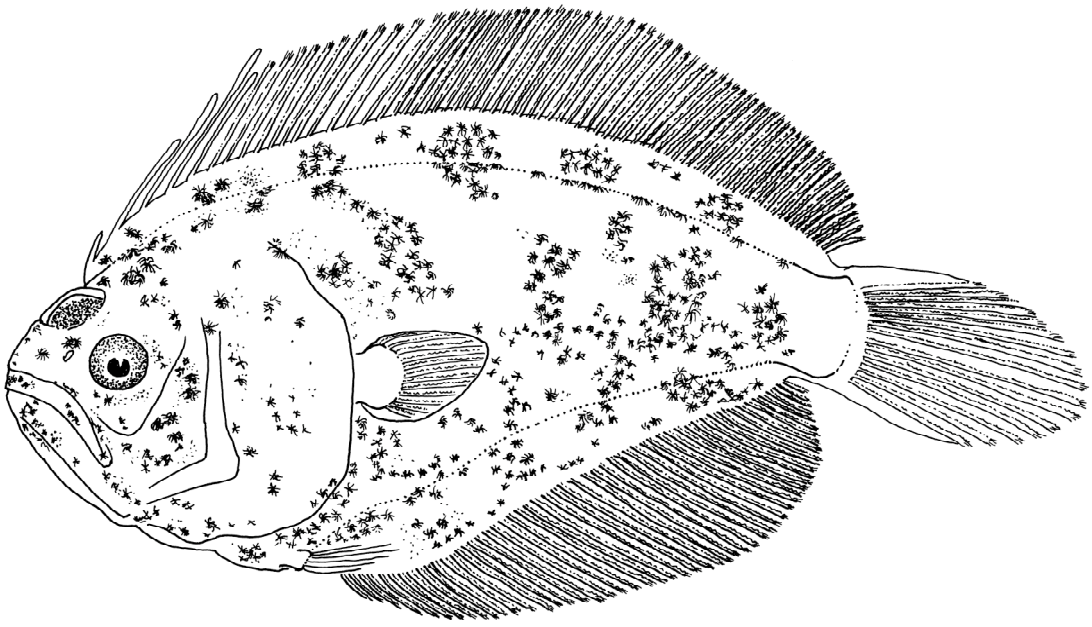


PARALICHTHYIDAE
Paralichthys adspersus (Fine flounder, Lenguado común, lenguado fino)
Postflexion

Appendix 6 (continued)

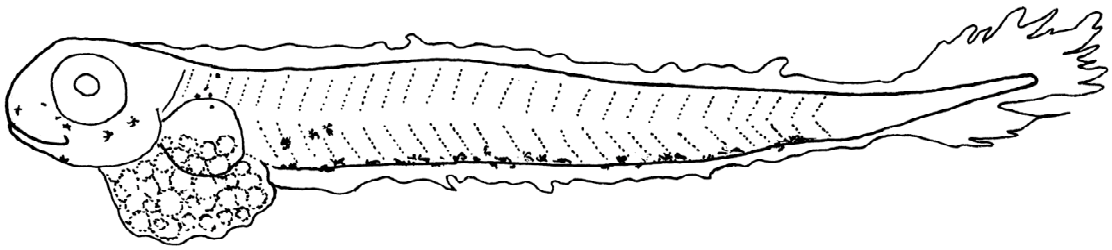


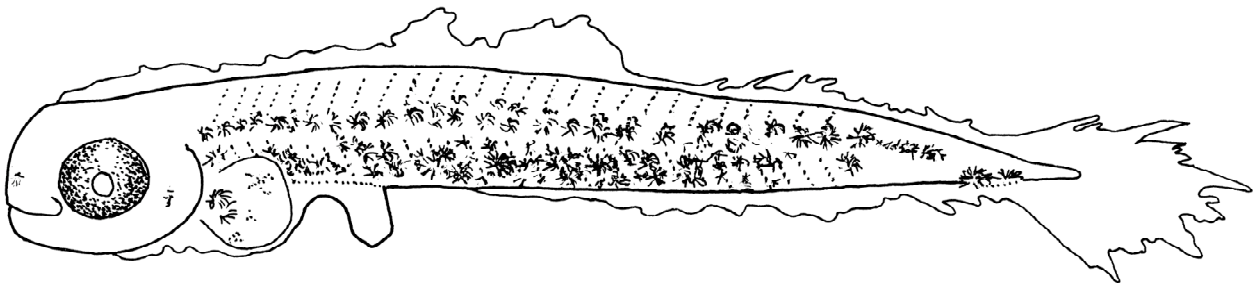
PARALICHTHYIDAE
Paralichthys adspersus (Fine flounder, Lenguado común, lenguado fino)
Postflexion



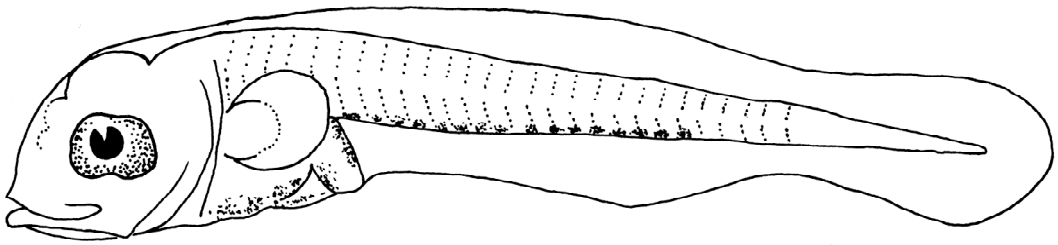
PARALICHTHYIDAE
Hippoglossina sp. (Spotted flounder, Lenguado ojon, lenguado pintado)
Postflexion

Appendix 6 (continued)



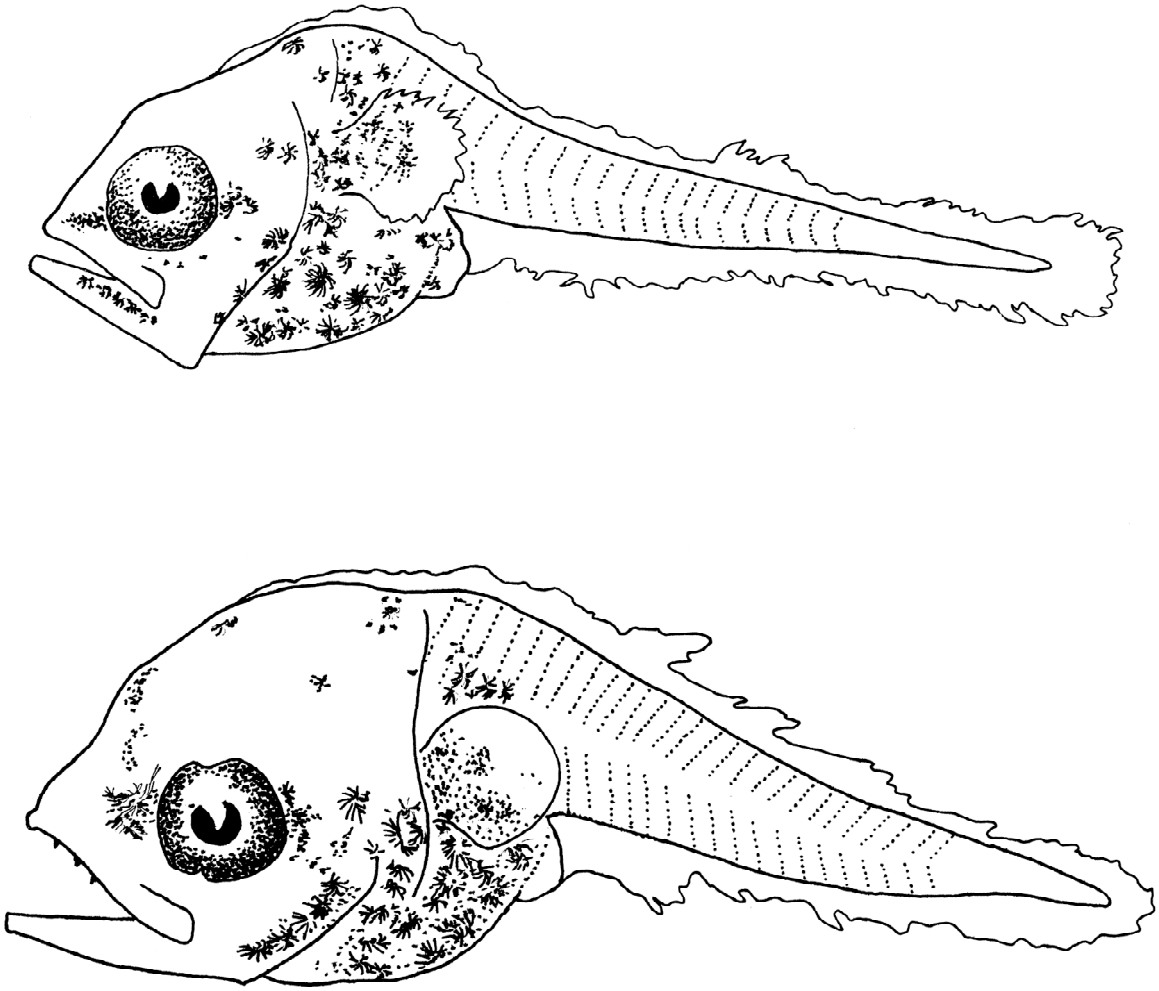


POMACENTRIDAE
Chromis sp. (Damselfishes, Sergeant majors, Castañuelas, Sargos de peña)
Preflexion



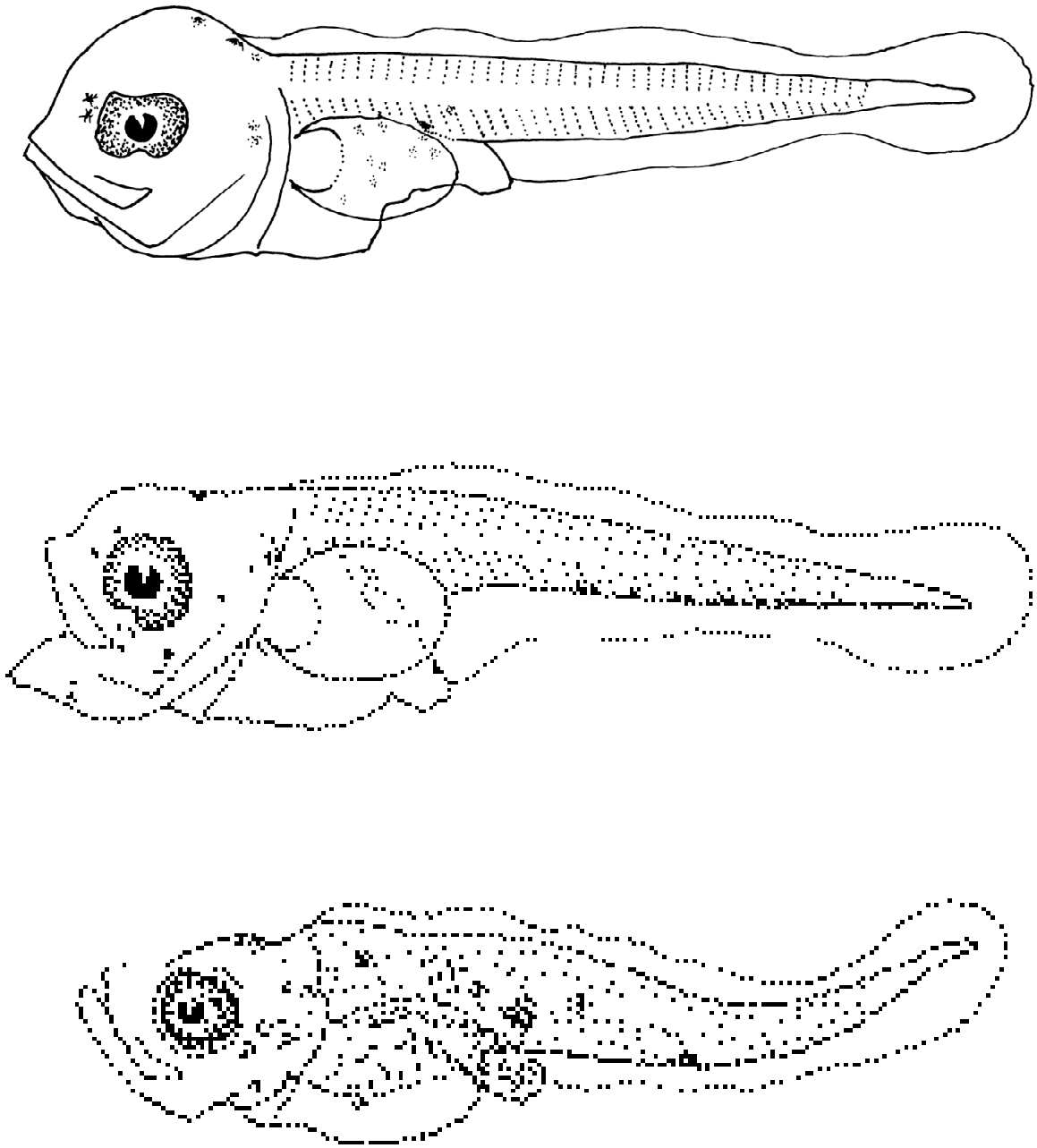
SCORPAENIDAE
Sebastes capensis (Scorpionfishes, Rockfishes, Diablos, Chamacos)
Preflexion

Appendix 6 (continued)



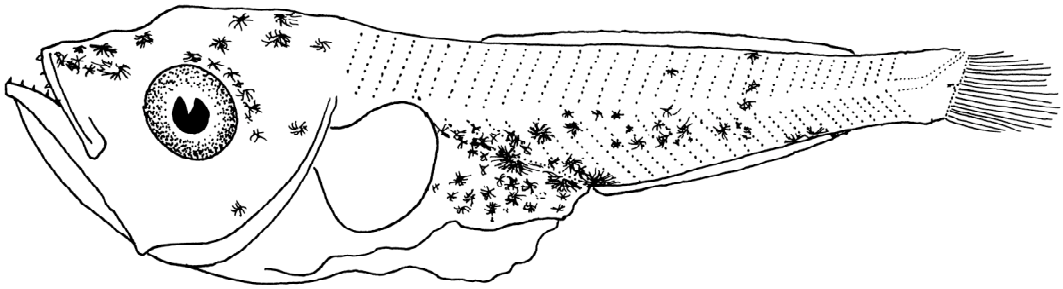
SCIAENIDAE
Sciaena sp. (Croaker, Drums, Corvinas, Lornas)
Preflexion

Appendix 6 (continued)

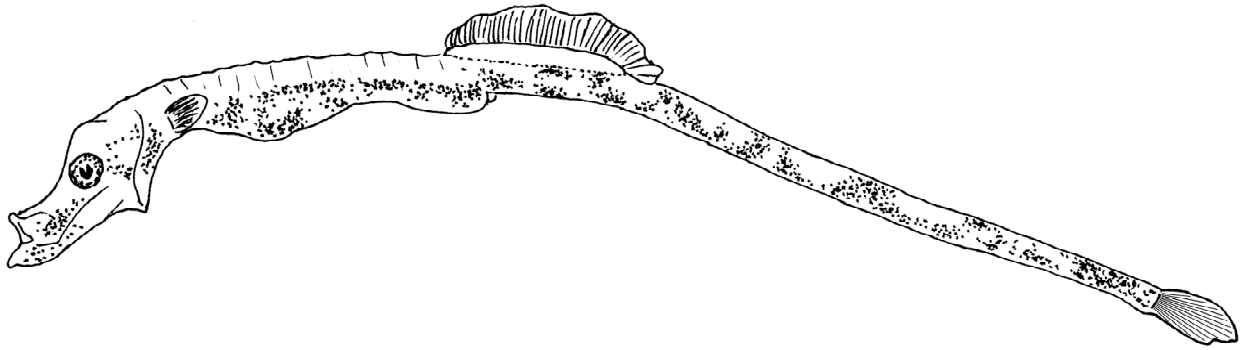


SCOMBRIDAE
Auxis sp. (Tunas, Mackerels, Bonitos, Atunes)
Preflexion

Appendix 6 (continued)



SPHYRAENIDAE
Sphyraena idiastes (Barracudas, Picudas)
Postflexion



SYNGNATHIDAE
Leptonotus blaivillianus (Pipefish, Pez pipa, Pipeta)
Postflexion

8.7 Appendix 7. Method of clearing and staining cartilage and bone in larvae, juvenile and adult fish (from Moser et al., 1984).

Steps	Length in mm, NL or SL: 10	20	30	40	50	60	70	80	90	100	200	300	400	500	>500
Fixation:															
10–15% formalin - marble chip buffered.	2 days								3 days			5 days, flesh removed on left side			
Dehydration:															
1. 50% distilled H_2O, 50% of 95% ethanol.	1 day				2 days				3 days			5 days			
2. Absolute ethanol (95% ethanol may be substituted).	1 day				2 days				3 days			7 days			
	one intermediate change														
Staining cartilage:															
100 ml solution: A. 70 ml absolute ethanol, 30 ml acetic acid, 20 mg alcian blue.	1 day										1½ days			2 days	
	Solution A										Solution B				
100 ml solution: B. 60 ml absolute ethanol, 40 ml acetic acid, 30 mg alcian blue.															
Neutralization:															
saturated sodium borate solution.	½ day										2 days				
									one intermediate change						
Bleaching:															
pigmented specimens only. 100 ml solution: 15 ml 3% H_2O_2, 85 ml 1% KOH.	20 min.			40 min.					1 hour			1½ hours			
Trypsin digestion:															
100 ml solution: 35 ml saturated sodium borate, 65 ml distilled H_2O, trypsin powder.	Keep in solution until 60% clear, change to fresh solution every 10 days														
Staining bone:															
1% KOH solution with alizarin red stain.	1 day								2 days			4 days			
Destaining:															
100 ml solution: 35 ml saturated sodium borate, 65 ml distilled H_2O, trypsin powder.	2 days			Change to fresh solution every 10 days until solution remains unstained and specimen is clear											
Preservation:															
30% glycerin and 70% of 1% KOH. 60% of glycerin and 40% of 1% KOH. 100% glycerin with thymol as final preservative*.	1 week				2 weeks						4 weeks				

* Direct sunlight and 100% glycerine help to clear and destain difficult specimens.