On the Occurrence of the Engraulid Fish, Stolephorus buccaneeri Strasburg, in the Oceanic Region of the Equatorial Western Pacific : Life History and Distribution

Ozawa, Takakazu
Fisheries Laboratory, Faculty of Agriculture, Kyushu University

Tsukahara, Hiroshi
Fisheries Laboratory, Faculty of Agriculture, Kyushu University

https://doi.org/10.5109/22827

出版情報：九州大学大学院農学研究院紀要. 17 (2), pp.151-171, 1973-03. Kyushu University
バージョン：
権利関係：

J. Fac. Agr., Kyushu Univ., 17, 151-171 (1973)

On the Occurrence of the Engraulid Fish, *Stolephorus buccaneeri* Strasburg, in the Oceanic Region of the Equatorial Western Pacific

— Life History and Distribution —

Takakazu Ozawa* and Hiroshi Tsukahara

Fisheries Laboratory, Faculty of Agriculture,
Kyushu University, Fukuoka

(Received July 2, 1972)

Larvae of *Stolephorus buccaneeri* previously reported only from coastal waters, were collected dominantly with larva nets in the oceanic regions of the Equatorial Western Pacific during the cruises of R/V Shunyō-maru and R/V Hakuhō-maru. The development from larva (3.2 mm SL) to adult (39.5 mm SL) is described. The following changes of body form are characteristic of engraulid fishes; slender body deepens, head becomes round and mouth inferior, dorsal and anal fins shift anteriorly; with rapid changes shortly after 15 mm SL, the juvenile assumes almost the adult form. The melanophores typical of the postlarva are restricted to the ventral surface and show strongly throughout development; those of the adult first appear at a late postlarval stage. It was found that after the late postlarval stage the developmental sequence is subject to intraspecific variation correlated with distribution, the more oceanic the fish the earlier the changes to adult form occur. In Hakuhō-maru samples, postlarva of just over 15 mm SL changes morphologically more rapidly, to reach the juvenile stage at about only 25 mm SL; the size of the adults is less than 40 mm SL.

Brain form of S. *buccaneeri* was compared with that of four other *Stolephorus* species taken in the neritic waters. The oblong telencephalon and relatively long bulbus olfactorius were found to be characteristic of S. *buccaneeri,* although intraspecific variation was found. The brain of the oceanic specimens is well separated from the skull and has a slender telencephalon, in contrast with that abutting on the skull and the oblong telencephalon in the neritic specimens.

The larval occurrence was independent of the direction of the surface currents and the composition of samples was similar in the oceanic regions. The results of collections by MTD horizontal closing nets in the upper 500 m indicate that these larvae are limited to surface water. It is concluded that S. *buccaneeri* probably inhabits and completes its life history both in oceanic and neritic waters throughout the whole West Pacific region. According to analysis by t-test, meristic counts did not show highly significant differences ($P \leq 0.01$) among 6 samples taken in different areas (three oceanic, the others neritic). The results support the assumption that the species may occur as an immigrant into neritic waters.

---

* Present address : Laboratory of Fisheries Resources, Faculty of Fisheries, Kagoshima University, Kagoshima, Japan.

I. INTRODUCTION

To study the biogeography of fish larvae, collections were made in the North and Equatorial Pacific Ocean during the R/V Hakuhō-maru Cruise KH-69-4, Ocean Research Institute, University of Tokyo. Using these samples, we have tried to elucidate the characteristics and boundaries of larval fish fauna. However, a prerequisite to these investigations is a knowledge of the biology of each species. Compared with neritic species, life history and ecological studies on oceanic fishes have been rather few to date. This is the case with ***Stolephorus buccaneeri*** Strasburg, a species collected dominantly in the oceanic region of the Equatorial Western Pacific by larva nets during the cruises of R/V Hakuhō-maru mentioned above and of R/V Shunyo-maru, Fisheries Agency of Japan.

The Indo-Pacific engraulid genus ***Stolephorus*** includes 14 species according to Ronquillo (see Whitehead, 1967 a and Tiews ***et al.*,** 1970). These small gregarious coastal fishes are of some commercial importance in this region, being used as food by the natives and as baitfish for tuna and skipjack fishing. Few studies on the biology of these species have been made; Whitehead (1965, 1967 a, b) commented on their systematics and Kow (1967) on their growth, etc., but as yet only the Hawaiian S. ***purpureus*** has received much attention (see Nakamura, 1970). In the case of their life history, only 7 species including S. ***buccaneeri (as zollingeri)*** have been studied from egg to prelarva by Delsman (1931) and S. *purpureus* from egg to adult by Yamashita (1951).

S. ***buccaneeri*** is fairly well distinguished from other ***Stolephorus*** species and is considered to be rather primitive member of the genus (Whitehead, 1967a). It has been reported from the coastal waters ranging from Hawaii in the east (Strasburg, 1960) to the east coast of south Africa in the west (Whitehead, 1967 a), i.e., across nearly the entire Indo-West Pacific region. We have studied in this paper the life history and the distribution of the species and discussed the morphological variations over its wide range.

II. COLLECTIONS AND MATERIALS

Tracks of two cruises and the abundance of S. ***buccaneeri*** larvae are shown in Fig. 1. The cruise of R/V Shunyo-maru was made from south west of Japan to north west of New Guinea and back, from November to December, 1961. On this cruise conical larva net (mouth diameter 2.0 m, length 6.0 m, mesh aperture in the one third rear part 0.5 mm) were towed simultaneously at the surface and sub-surface ***(20*** to 30 m deep) for ***20*** min., four times a day. In Fig. 1, only the abundance of larvae at the surface and at night is illustrated. The Hakuhō-maru followed longitude 155°W, descending from 50°N to 15°S, turned westward and then sailed on a course from Tahiti to Japan via Western Samoa from August to November, 1969 (Ocean Research Institute, 1970). The cylindrical-conical larva net (mouth diameter 1.6 m, length 7.5 m, mesh aperture 0.5 mm) was hauled at the surface for ***20*** min. every night. On both cruises the towing speed was 2 knots and the sea depth at all sampling stations of S. ***buccaneeri*** was over ***3,000*** m. The time of sampling was progressively later from east to west.

After initial preservation in 10% formalin solution on board, fish eggs and

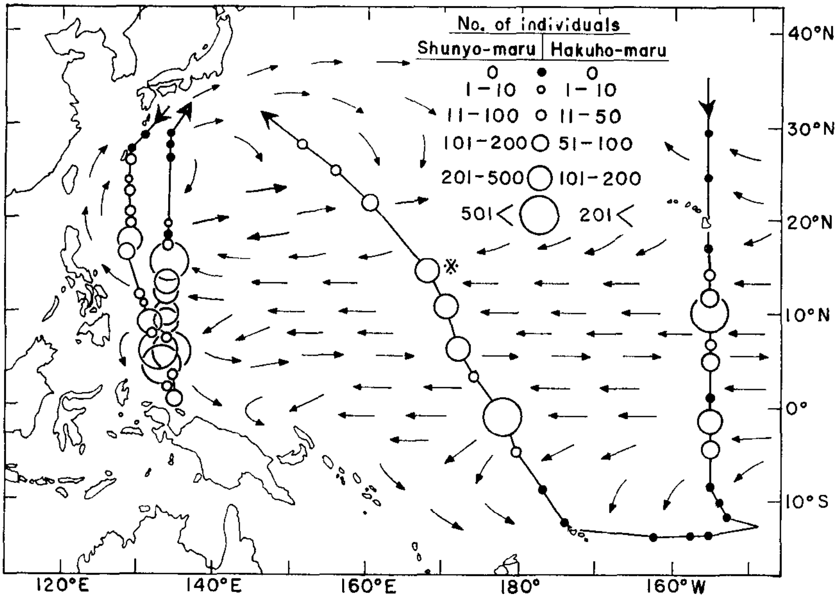

Fig. 1. Cruise tracks by R/V Shunyō-maru (left) and by R/V Hakuhō-maru (right), and the abundance of *Stolephorus buccaneeri* larvae.
Arrows indicate the direction of surface currents after Sverdrup *et al.* (1967) slightly modified on Uda and Hasunuma (1969). Locality with asterisk denotes the catch of one adult in R/V Shunyō-maru another cruise.

larvae were later transfered to 70 % alcohol in the laboratory. The specimens of S. *buccaneeri* mainly comprised postlarvae, ranging from 3.0 to 31.2 mm in standard length (SL, the distance from the tip of head to the end of notochord or hypurals) . In addition to these, we have 7 other specimens of S. ***buccaneeri:*** three adults (61.1 — 71.4 mm SL) captured at Palau Island in April, 1967; an adult (39.5 mm SL — see Description below) ; a juvenile (30.9 mm SL) collected at the estuary of the Sendai River, Kagoshima Prefecture, in September, 1970; an adult (44.5 mm SL) and a young (33.0 mm SL) taken at Suruga Bay during the end of summer of 1967.

III. LIFE HISTORY

(a) **Description of adult**

Based on a female, 39.5 mm SL (47.0 mm in total length) taken by larva net, on May 7, 1961, during an earlier Shunyō-maru cruise (May — June). The locality (14°32'N ; 168°42'E — see asterisk, Fig. 1) is about the same as one in the Hakuhō-maru cruise, so that this specimen can be equated with those of the Hakuhō-maru cruise.

The lateral view of the specimen is shown in Fig. 2 J. Body elongate, moderately compressed. Head conical from both lateral and dorso-ventral views, snout smoothly pointed, mouth large and inferior. Maxilla with two supra-maxillae, extending to mandibular joint, expanded posteriorly, its tip truncate.

Slender urohyal plate, urohyal exposed behind hind border of branchiostegal membrane. Fine teeth on pre-maxillary, maxillary, mandible, palatine, hyoids, pterygoids and vomer. Pseudobranchiae well developed ; both faces of gill rakers finely denticulate. Five abdominal scutes, lying below pectoral fin. Anal origin at some distance behind last dorsal ray. Caudal forked, the sixth ray from the top and bottom with a transparent alar flap. No lateral line ; deciduous cycloid scales, almost lost from whole body, *40* or 41 in a longitudinal series, 9 in a transverse series; an elongate axillary scale above pectoral and pelvic base, not pigmented.

Mature ovarian eggs (maximum 0.36 mm x 0.19 mm) similar in shape to those described by Strasburg (1960) and Hayashi and Tadokoro (1962 a-as *zollingeri).*

Color in alcohol straw with a prominent pigmented band (possibly silver in life) lengthwise from gill opening to caudal base, the band about equal to eye diameter in width but narrower at both ends ; tip of snout and mandible blackish, a spray of fine black dots on occipito-parietal region and on upper preopercle; scale pockets above lateral band margined in black ; dorsal and caudal rays black-spotted ; a row of black spots along anal base and on mid-ventral line of caudal base.

Dorsal rays 12 to 14, anal rays 14 to 16, vertebrae (including urostyle) 23 to 25+17 to 19-41 to 43 (these counts include those for 84 larval specimens from the Hakuhō-maru cruise) ; pectoral 14, ventral 7, branchiostegals 12, gill rakers on first gill arch 16+2+24=42.

The following measurements are expressed in thousandths of standard length. Head 256, snout 50, postorbital 132, upper jaw 159, eye diameter 68, snout to dorsal origin 550, snout to anal origin 636, snout to pelvic base 442, snout to pectoral base 268, maximum depth just before pelvic fin base 182, maximum body width 122, least depth of caudal peduncle 84, longest pectoral ray 147, longest pelvic ray 96, distance from tip of pectoral fin to pelvic base 35.

The systematics of ***Stolephorus*** species have posed many problems in the past. Recently, Whitehead (1965) and Ronquillo (see Whitehead, 1967 a and Tiews ***et al.,*** 1970) have re-examined this difficult genus and have proposed a key to all species using new and apparently stable characters. We have generally followed their key, in conjunction with those of Weber and De Beaufort (1913), Hardenberg (1934), Fowler (1941), Shen (1959) and Munro (1967). It should be noted that these latter authors have used Bleeker's name ***zollingeri*** for ***buccaneeri;*** the types of the former are in fact ***Engraulis japonica*** (Whitehead ***et al.,*** 1966).

The specimen described here is identified as S. ***buccaneeri*** from the keys of mentioned above (except that of Fowler). The descriptions of these authors (except Fowler and Munro) and of Strasburg (1960) and Hayashi and Tadokoro (1962 a — as ***zollingeri)*** strongly resemble that given here.

(b) Description of developmental stages

The developmental stages studied are from postlarva to adult in this paper, and eggs and prelarvae were not collected. Eggs and prelarvae were described (as *zollingeri*) by Delsman (1931), and the remaining ontological [sequence can be completed in this paper.

Postlarval stage

1) 3.2 mm SL (Fig. 2 A). Judging from the description of Delsman, larvae of this size seem to have just entered the postlarval stage. The slender larva has straightened out to the tip of notochord, the cells of which, since not overlaid by cross striations, may be seen clearly. The yolk is already absorbed. The anus, lying below about the 31st myomere, is set very far back, about four-fifths

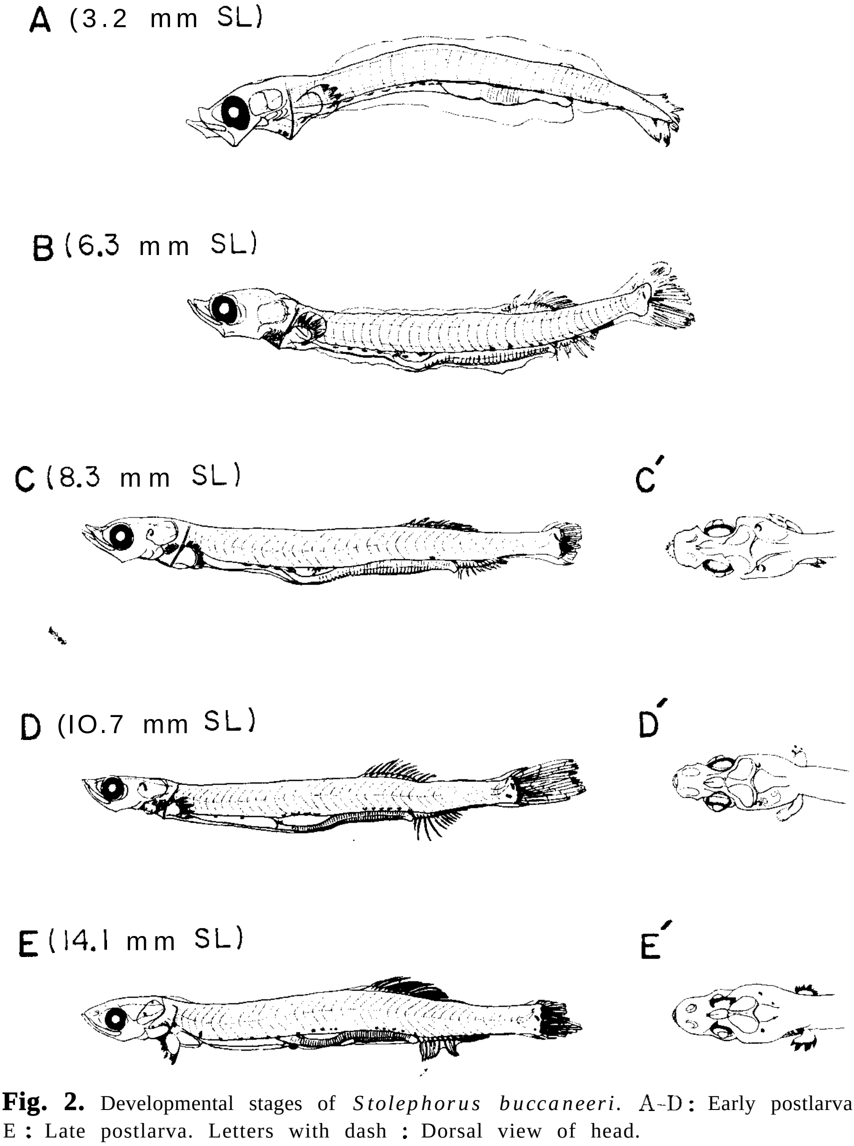

Fig. 2. Developmental stages of *Stolephorus buccaneeri*. A-D: Early postlarva. E: Late postlarva. Letters with dash: Dorsal view of head.

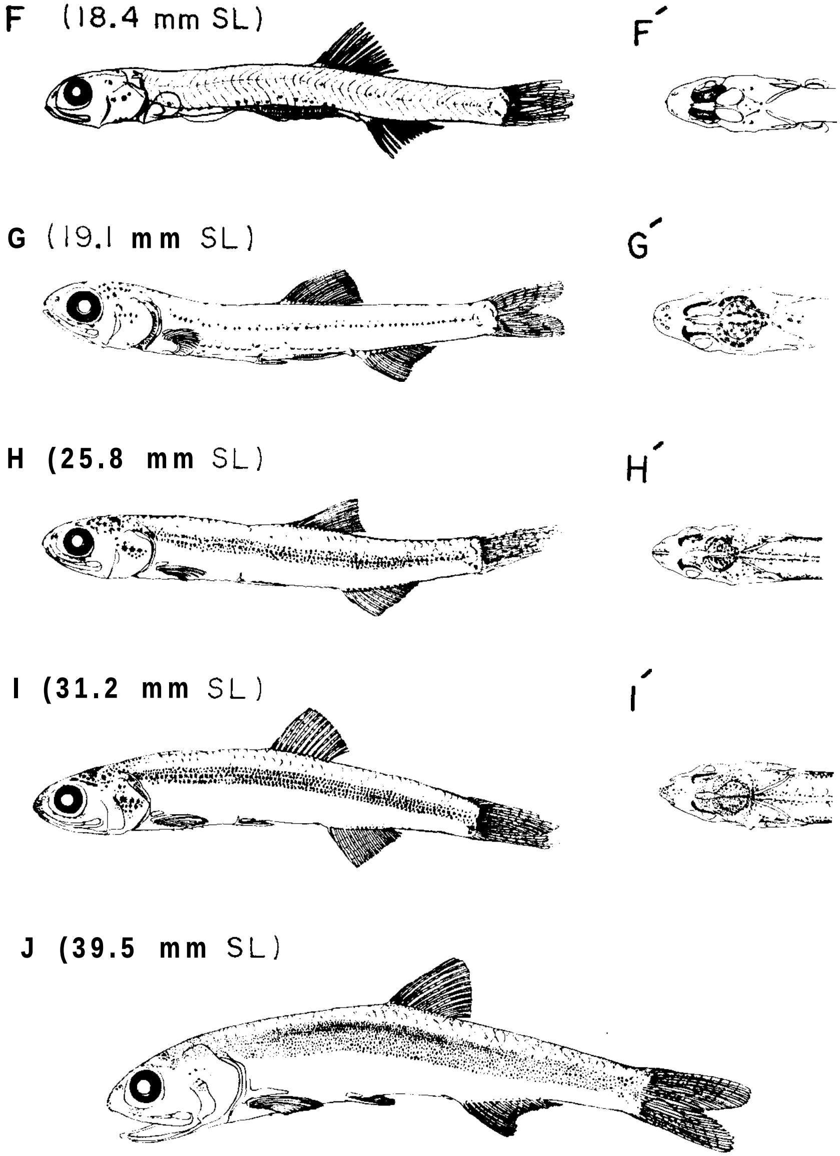

Fig. 2. (continued). Developmental stages of ***Stolephorus buccaneeri.*** F, G : Late postlarva. II : Juvenile. I : Young. J : Adult. Letters with dash : Dorsal view of head.

of the distance to caudal base. The jaws are oblique and the posterior tip of the maxilla extends somewhat past the anterior margin of eye, which is oval. The gill arches are naked, being free of both gill rakers and filaments. The intestine appears thick and obscurely convoluted. The upper median fin-fold originates at the nape, the lower one below the pectoral fin ; the fin-fold at the tip of notochord seems to be differentiating. Only the base of dorsal fin is present; both the base of the anal fin and the air-bladder first appear when the fish reaches about 4.0 mm SL.

Elongated melanophores in row or spots are limited to the ventral surface, a characteristic condition of the larval stage, but they later show marked changes during subsequent growth stages. The melanophores along the median line of the isthmus seem to be separated into two or three spots in lateral view, but are continuous when viewed ventrally. Later, they extend anteriorly but disappear when the fish becomes adult. Melanophores along the stomach diminish in number, disappearing when the fish reaches about 15 mm SL. On the mid-ventral line of the intestine can be found an obscure line of slender melanophores, which are destined to vanish at about 7 mm SL. A few spots above the posterior half of the intestine are faintly discernible, but the one near the anus is very distinct. One melanophore lies on the future anal fin base, two are on the lower edge of the caudal peduncle, and one is found on the lower lobe of the caudal fin.

2) 6.3 **mm SL** (Fig. 2 B). Marked changes have taken place by the size of this larva. The notochord is bent and the hypurals are developing. The air-bladder has broadened and lengthened, from the 14th to the 17th myomere in this specimen. The rays in the dorsal, anal and caudal fins are differentiated well enough to permit enumeration ; the caudal fin not forked. The depth of median fin-folds becomes less. The tip of lower jaw remains terminal and pointed. The posterior tip of the maxilla has moved back to somewhat in front of the center of the eye, which is still oval shaped. Minute denticulations, about 5 on the maxilla and 3 on the lower jaw, can be seen. The gill arches remain exposed. One to three gill rakers on the lower limb of first arch and gill filaments on the 2nd to 4th arch have appeared.

A conspicuous black melanophore occurs on the mid-point of cleithrum, an expanded one occurs on the air-bladder and an oblique one on the upper hypural fan. The row of melanophores on the mid-ventral line of the intestine is fading away and the two spots on the caudal peduncle have become continuous.

3) **8.3 mm SL** (Fig. 2 C). Flap of opercle and also nostrils first appear at this size. The anus has moved slightly forward, to 30th myomere. Twelve rays in both dorsal and anal can be counted and the principal caudal rays are apparently present.

A spotted melanophore on the anterior margin of the auditory vesicle and one on the lower part of the cleithrum have now appeared, but the row along the mid-ventral line of the intestine has already disappeared. Melanophores in row on the stomach are either horizontally expanded or shrunken depending on specimen.

4) **10.7** mm **SL** (Fig. 2 D). Larvae of this size show somewhat pronounced changes of body form. Cross striations along the body have disappeared. The posterior tip of the maxilla terminates below the center of pupil. The pelvic fin bud is first seen below the 15th myomere at the junction of the stomach and the intestine and this position does not vary appreciably from this stage through to

the adult. Two or three dorsal rays lie behind a vertical from the anus. In all of the foregoing stages, the tip of the snout appears truncated in dorsal view.

A black pigment has appeared on the upper tip of the notochord and on the lower hypural fan. The melanophore under the pectoral fin has disappeared and the row of melanophores along the stomach is also fading. One or two melanophores may be recognizable on upper part of the caudal peduncle in some specimens. The pigment on the anal base tends to split into spots.

5) 14.1 mm SL (Fig. 2 E). Tip of the snout has become rounded, with the lower jaw still terminal. The body has slightly deepened. The posterior tip of maxilla reachs to below the posterior margin of eye. The anus has advanced to the 29th myomere. Dorsal and anal fin rays are now definitive, both with 14 rays in this specimen. About 4 pelvic fin rays can be counted.

In addition to pigmentation previously mentioned, new melanophores occur on the top of auditory vesicle and under the opercle. A row of melanophores now re-appears along the ventral line of the body dorsal to stomach, of which the most anterior one is very prominent.

6) 18.4 mm SL (Fig. 2 F). Late postlarval fishes, larger than 15 mm SL, show marked changes which have wide variation depending on the sampling area. The specimens caught in the Shunyō-maru cruise, which are described here, reveal less marked changes than those in the Hakuhō-maru (see DISCUSSION).

The tip of snout has become more rounded, but the lower jaw still projects slightly beyond the upper, which now has 2 supra-maxillae. The posterior tip of the maxilla extends beyond the posterior margin of eye. The nostril has separated into two pores. The opercle has expanded to cover the gill arches. In all of the foregoing stages, the alimentary tract is suspended by the dorsal mesentery. The anus has advanced to the 28th myomere and 2 or 3 rays of the dorsal are still behind the vertical from the anus. The pelvic fin rays are now definitive, 7. On the 6th principal rays from the top and bottom of the caudal fin, a transparent alar flap has appeared. It seems that just above this size, the scales will make their first appearence in the caudal region. The scale sequence of formation could not be traced exactly because of easy desquamation.

New spots of melanophores are now found on the opercle, just behind the pelvic fin base, and on the base of the dorsal fin. A faint row of melanophores along the mid-lateral part in the posterior half of the body is the first indication of silver band in the adult.

7) 19.1 mm SL (Fig. 2 G) The specimen described here, from the Hakuhō-maru cruise, is further developed than the previous one, in spite of being almost the same size. With rapid changes through the stages shown in Figs. 2 F and G, the postlarvae of the Hakuhō-maru cruise metamorphose into the juvenile stage. On the other hand, those taken in the Shunyo-maru cruise show relatively retarded development, even though the largest specimen is 22.7 mm SL. This may also be the case of the juvenile (30.9 mm SL) caught at the estuary of Sendai River, which is similar in pigmentation to the specimen described here. The following descriptions are based only on the Hakuhō-maru sample.

The larva of this size begins t-o resemble the adult with the typical inferior mouth and conical head. The body is deepening and the alimentary tract has been almost integrated within the body, leaving the intestine still exposed. It is still difficult to count the pectoral fin rays (9 in this specimen). Above the pectoral base, an elongated axillary scale has started to appear. The last dorsal ray has moved forward to above or before the anus. A small median fin-fold remains just before the dorsal fin base.

The pigmentation has begun to approach the adult condition. Melanophores on the dorsal part of the head, on the opercle, along the mid-lateral part of the body and on the caudal fin have become more pronounced. All melanophores dorsal to the alimentary tract are now located higher on the body, being visible through the body wall. The melanophores characteristic of the adult are beginning to appear around the tip of snout, on the tip of the lower jaw, both below and behind the eye, on the mid-dorsal line from the nape to caudal fin base, and on the first 5 or 6 dorsal rays.

Juvenile stage

8) **25.8 mm SL** (Fig. 2 H). At about **25** mm SL, the fish has all the features of the juvenile stage, that is to say, the body is wholly covered with scales (judging from the existance of scale pockets), the pectoral fin ray count is constant. The maxilla extends far beyond the posterior margin of eye, the opercle entirely covers the gill filaments, and the proportions of the body are almost those of the adult (for example, the distance from tip of snout to anus is 66% of SL). Three abdominal scutes are present below the pectoral fin.

Adult pigmentation has become more prominent, and the melanophores on the alimentary tract are difficult to detect through the body wall.

Young stage

9) 31.2 mm SL (Fig. **2** I). A specimen of 31.2 mm SL has most of the adult characteristics. The body has become deeper, especially anterior to the dorsal fin. The conical, projecting snout is fully developed and the posterior tip of the maxilla is as in the adult, i.e., reaching to the mandibular joint. Four abdominal scutes are found. An elongated axillary scale can be seen at the pelvic base, but the urohyal plate characteristic of the species has not yet developed.

Pigmentation along isthmus, on cleithrum and at the pelvic fin base has been progressively disappearing, but that on the anal base and along the lower edge of the caudal pcduncle tends to remain through to the adult stage.

Adult stage

10) 39.5 mm SL (Fig. 2 J). The adult of the species has been mentioned previously.

(c) Discussion

As seen in the explanations to Figs. 2 F and G, the late postlarval development of S. ***buccaneeri*** seems to show some variation. The specimens caught in the Hakuhō-maru cruise metamorphose at about **25** mm SL, whereas the postlarvae described by Hayashi and Tadokoro (1962 a) had a total length of 38 mm SL* and the specimen illustrated by them (34 mm in total length) resembles our sample of 18.4 mm SL (Fig. 2 F). And as stated before, the juvenile (30.9 mm SL) taken in the estuary of Sendai River is analogous in pigmentation to the specimen (19.1 mm SL) described in Fig. 2 G.

In Fig. 3, is plotted the relative growth of head length (from the tip of snout to the posterior end of opercle), of upper jaw length and of pectoral-pelvic interspace (from the tip of pectoral fin to the base of pelvic) in hundredths of standard length, being separated into two samples; the first from the Hakuhō-maru cruise and the second from the Shunyō-maru cruise. The two samples from the former cruise from different sampling areas are combined, since difference in their development could not be found. For head length and pectoral-pelvic interspace, data deduced from Matsui (1963: Figs. 8 and 9) are added. In all three characters can be seen slight differences between samples from the two cruises. Although marked changes to the adult form occur when the fish reaches about 15 mm SL, they are more rapid in the sample of Hakuhō-maru cruise than that of Shunyō-maru cruise. The head length of the former sample reaches its maximum relative proportion between 20 to 25 mm SL and thereafter gradually decreases. On the other hand, in the case of the Shunyō-maru sample (which are less than 23 mm SL), the change to the adult proportions seems to

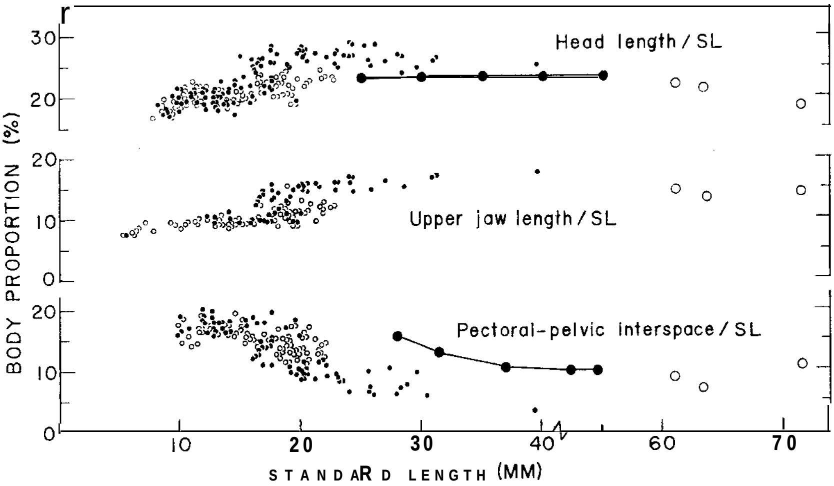

Fig. 3. Changes of body proportion of ***Stolephorus buccaneeri*** showing the variations among sampling areas.

Small white circle : Sample in R/V Shunyō-maru cruise. Small black circle : Sample in R/V Hakuhb-maru cruise. Large white circle : Sample caught at Palau Island. Large black circle : Sample in Hawaii deduced from Figs. 8 and 9 of Matsui (1963).

It seems that the term 'postlarva' of Hayashi and Tadokoro is identical with 'juvenile' of ours (Dr. S. Hayashi, personal communication). We had the chance to examine the specimen of 33 mm SL taken at Suruga Bay in 1967, and found that it was young or immature stage.

occur at a larger size and may not reach such a high relative figure, as shown by the Hawaiian sample. If our two samples are compared with that of Hawaii, the discrepancy in pectoral-pelvic interspace is clearer than in head and jaw lengths, and there is no overlap with the Hawaiian or other samples, even at adult size. However, it must be noted that in the Hawaiian sample the presence of intermediates between the two species S. ***buccaneer?*** and S. ***purpureus*** (in a comparison of body proportions) raised doubts as to the designation of S. ***buccaneeri*** as a distinct species (Matsui, 1963). According to the present authors, this confusion might have arisen from either hybridization of the two species or the overlooking of more stable characters. The latter is supported by the general variability in body proportions in engraulid fishes and by the highly significant meristic counts in Matsui's sample among others (see Table 4).

Variation correlated with different sampling areas is also found in size at maturity; less than **40** mm SL in this paper, more than 45 mm SL in Hawaii (Strasburg, 1960), probably more than 55 mm SL in Japan (Hayashi and Tadokoro, 1962 a) and 65 mm TL in Manila Bay (Tiews ***et al.,*** 1970). The values for three

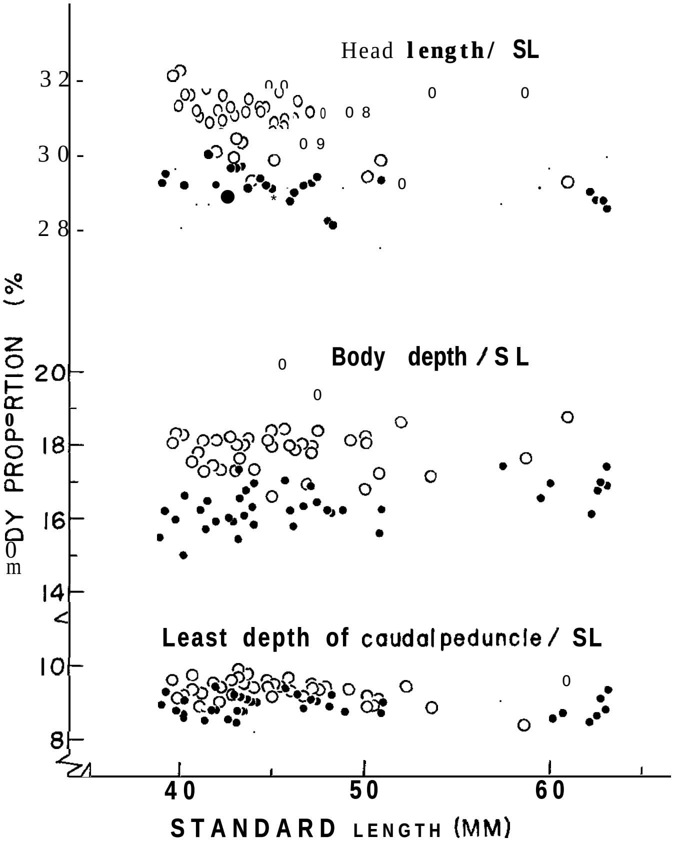

Fig. 4. Proportional difference of body form of *Engraulis* ***japonica*** taken at two areas. White circle : Sample at Fukuyama City facing Seto Inland Sea. Black circle : Sample at Shibushi Bay facing the Pacific Ocean.

Table 1. Difference of body proportion of ***Stolephorus heterolobus*** taken at two areas (expressed as hundredths of standard length).

Area	No.	SL (mm)	LGR	Vertebrae	HL/SL	UL/SL
Palau Island	7	39.9-72.7	25-28	43, 44	22.5-25.4	19.2-21.3
Ryūkyū Island	a	46.0-59.6	28-30	42-44	25.5-27.9	21.3-24.2

No. : Number of specimens. SL : Standard length.
LGR : Number of lower gill rakers. HI, : Head length.
UL : Upper jaw length.

full grown specimens taken at Palau Island are shown in Fig. 3. Though curves linking these with the other samples could be drawn, it might be misleading because it would combine samples from different areas.

Although uniformity of early development is found in most species, it is possible that species which have a wide range may exhibit discrepancies in early development corresponding to various environmental conditions. For example, Fage (1940) cited the case of the flatfish, *Arnoglossus* ***laterna,*** whose larvae metamorphose at a length of 16 mm ***sur les côtes de Hollande*****, 21** to 26 mm ***à l'entrée occidentale de la Manche*** and 26 to 30 mm ***dans le golfe de Gascogne.*** In *Engraulis japonica*, Nakai ***et al.*** (1962) stated that postlarvae taken in coastal waters have a larger body depth than those taken offshore. Also in ***E. japonica,*** Uchida ***et al.*** (1958) reported a difference in body length at which the fishes attain juvenile stage, the coastal specimen being smaller than the offshore one. In Fig. 4, an example of immature fish is given. The fishes with the larger body proportions were caught at Fukuyama City facing Seto Inland Sea and are surely identical with the coastal type of Nakai ***et al.*** and Uchida. Those having lower proportions were taken at Shibushi Bay facing the Pacific Ocean, and are possibly the offshore type of the above authors. Though the latter locality is shallow coastal water, it was said by Asami (1958) that the fish were offshore in origin. In ***Sardinops melanosticta,*** juveniles taken along the coast of Japan Sea are denser colored than those taken along the Pacific coast of Japan, supposedly with the difference of solar rays in these waters (Aikawa, 1961: p. 94).

Let us cite an example of pelagic or mesopelagic fish, ***Vinciguerria lucetia,*** family Gonostomatidae, which is one of the most abundant fishes in the eastern North Pacific between the Equator and about 35°N latitude: specimens of ***V. lucetia*** metamorphose at a smaller size in the area south of 25°N latitude than in the northern part of its range (Ahlstrom and Counts, 1958: p. 372).

In Table 1, the body proportion of two samples of ***Stolephorus heterolobus*** are compared. The same variation as in ***E. japonica*** can be observed clearly. If body proportions only are considered, the specimens with larger proportions fit 'Species A' of Ronquillo (see Whitehead, 1967 a, b and Tiews ***et al.,*** 1970 ; synonym of ***S. devisi*** in a recent letter from Dr. P. J. Whitehead). From the experimental rearing of ***Salvelinus fontinalis, Salmo gairdneri, Coregonus clupeiformis,*** etc., Martin (1949) ascertained the variation in relative growth and indicated the direction and conditions of the phenomenon, e.g., proportion of head length is larger in fish reared at higher temperatures or with deficient food.

These facts suggest that the developmental phase may be variable, especially in engraulid fishes due to their wide distribution. This may be the case in S. ***buccaneeri.*** In fact, it has wider distribution than other engraulid fishes, not only in neritic but also in oceanic (see DISTRIBUTION). Returning to the variations in Fig. 3, it is noticed that they vary such that the more oceanic the fish, the earlier the change to adult form occurs. And it may be possible that the metamorphosis is more retarded in the larvae that migrate or are transported into coastal waters by ocean currents, such as the large postlarva of Hayashi and Tadokoro (1962 a) supposedly by the Kuroshio Current into Japanese coastal waters (Hayashi and Tadokoro, 1962 b). If it is recognized that these variations are intraspecific, then the difference in pectoral-pelvic interspace might be the result of the combination of different relative growths. It is, however, unknown whether the variety in development is continuous from oceanic to neritic. Delsman (1931) described two type of eggs of S. ***buccaneeri,*** under the impression that the longer variety might be called the more oceanic of the two, though both were found somewhat further from the coast than those of other ***Stolephorus*** species. Moreover, all a year-round resident population of S. ***buccaneer-i*** which spawns in the deep part near the fishing grounds ***is*** reported in Manila Bay (Tiews et ***al.,*** 1970). Even if the true neritic type exists, the specimens of Hawaii added in Fig. 3 may be inshore immigrants from oceanic waters, since the true neritic species, ***S. purpureus,*** dominates in Hawaiian waters. Although incomplete owing to shortage of data, the above remarks could support the supposition of the existence of two ecatypes, that is to say, a neritic and an oceanic type.

The development of ***S. buccaneeri*** from early postlarva to adult is described in this paper, being based on the samples taken in the oceanic areas. It is similar to that of the related species, S. ***purpureus*** (Yamashita, 1951) and ***E. japonica*** (Uchida ***et al.,*** 1958). If the larvae studied here is identified as S. ***buccaneeri*** and their distribution is continuous, then the variation in development is intraspecific, although its direction is the reverse of that found in ***E. japonica.*** This different phenomenon may result from the difference in habitat ; neritic for ***E. japonica*** and perhaps oceanic for ***S. buccaneeri.***

IV. BRAIN FORM

Uchihashi (1953) has demonstrated the parallelism of the brain form to the ecology in teleosts. As one of the biological characteristics, we examined the brain of S. ***buccaneeri.*** Only gross aspects will be mentioned here, indicating typical difference between oceanic and neritic specimens. External brain form in the adult (39.5 mm SL) taken in the oceanic region (see Description of adult) is shown in Fig. 5. At a glance, the brain is very similar to that of ***E. japonica*** in the 2nd stage ***(40-60*** mm TL) defined by Ogawa (1967). It looks shrunken and is well separated from the skull. The telencephalon is quite slender and the bulbus olfactorius is fairly long. In lateral view, the brain as a whole is flattened, club-shaped, showing that the cerebellum is not yet fully developed.

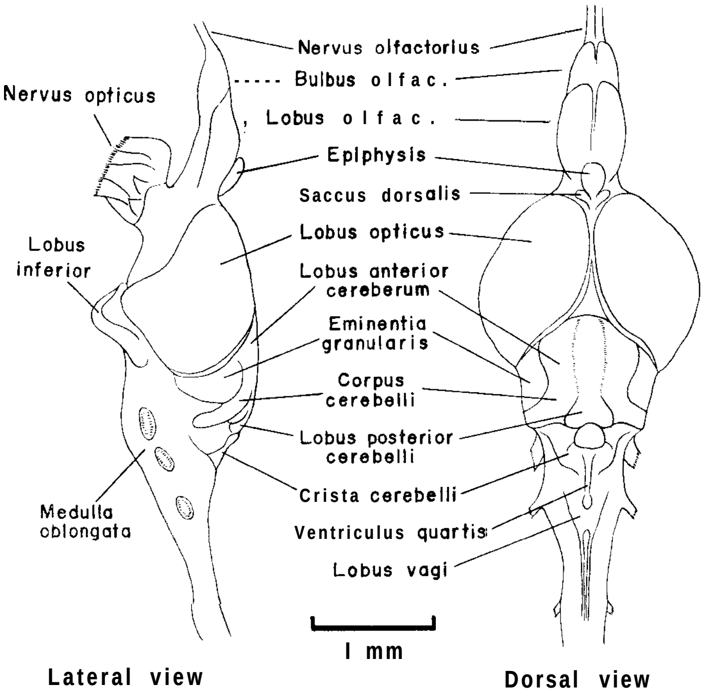

Fig. 5. The brain form of S. ***buccaneer-i*** (adult of 39.5 mm SL) taken at oceanic waters, the locality of which is indicated in Fig. 3.

On the other hand, as seen in Fig. 6, the brain of a coastal specimen (adult of 44.5 mm SL) taken at Suruga Bay during the end of summer of 1967, shows marked differences from that mentioned above. The brain is well developed to abut on the skull and the telencephalon fairly robust (lobus olfactorius of more grown specimen, 53.3 mm SL, taken at Palau Island in April, '67, have a round shape). In lateral view, it takes on a mallet-shape, resulting from the growth of the cerebellum. As far as we have investigated, it seems that the brain of oceanic specimens is, somehow, retarded in its development. In dorsal view, the development of the brain is described briefly in Figs. 2 C'-I'.

In the brains of Japanese teleosts, Uchihashi (1953) found that the space between the brain and the skull becomes filled up by fatty tissue as they dwell deeper. The brain of the fishes belonging to the genus ***Myctophum,*** Myctophidae, which are representatives of mesopelagic fishes and are night migrators at surface waters, is surrounded by a great deal of fatty tissue in adult specimens, while that of young shows the same aspect as the oceanic S. ***buccaneeri*** stated above (unpublished). In the brain of the latter, it is uncertain whether the fatty tissue can be found in more grown specimens as is found in ***Myctophum.***

The brain of 5 species of ***Stolephorus*** taken in coastal waters are too similar to detect the distinguishing characters, except in the case of S. ***buccaneeri*** which has an oblong telencephalon and a relatively long bulbus olfactorius (Fig. 6). These characteristics of brain form may have specific and phylogenetic impor-

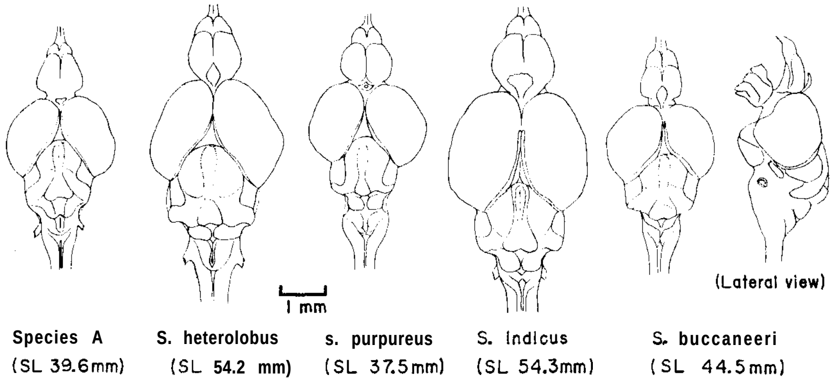

Fig. 6. The dorsal view of brains of 5 ***Stolephorus*** species taken at neritic waters. The lateral view is appended on *S.* ***buccaneeri*** alone. Species A, see Whitehead (1967 a) and Tiews et al. (1970).

tance, because S. ***heterolobus,*** Species A and S. ***purpureus,*** which all have a triangular telencephalon and short bulbus olfactorius, are the closest relatives of S. ***buccaneeri*** according to Ronquillo (see Whitehead, 1967 a and Tiews ***et al.,*** 1970).

V. DISTRIBUTION

(a) **Abundance of larvae**

It is a general phenomenon that the larvae of marine animals, such as well-known European eel, ***Anguilla anguilla,*** are transported over the oceans by surface currents and are spread out from spawning areas (Thorson, 1961). In Fig. 1, the direction of surface currents after Sverdrup ***et al.*** (1967), slightly modified by Uda and Hasunuma (1969) are given. In the region where the larvae of S. ***buccaneeri*** occurred most abundantly, three equatorial currents in opposite directions have been recognized ; the North and the South Equatorial Currents which flow westward and the Equatorial Countercurrent which flows eastward.

Although the larvae decrease northwards, they are distributed uniformly over the three areas regardless of the direction of the surface currents, that is to say, there is no indication of larvae being transported from a spawning area.

Table. 2 Comparison of composition of *S.* ***buccaneeri*** larvae among 3 areas in Fig. 1.

Area	No. of station	No. of individuals		No. of individ./ no. of total individ. (%)		Range of SL (mm)
		Average	Range	Average	Range	
A	3.2	102.3	0— 408	44.7	0-99.1	4.6-30.6
B	9	91.5	10— 311	68.2	3.3-92.3	3.2-25.1
C	27	440.7	0-4245	59.2	0-98.3	3.1-22.7

A, south of Hawaii ; B, between Western Samoa and Japan ; C. between southern Japan and north west of New Guinea. No. of individuals: Number of the larvae per haul. No. of total individ. : Total number of larvae per-haul SL : Standard length.

This picture is supported by a comparison of the composition of larvae between sampling areas (Table 2). In this table, the area is divided into 3 lots; south of Hawaii (A), from western Samoa to Japan (B) and from southern Japan to north west of New Guinea (C). (At the station 10°N ; 155°W, five collectons were made, and in Fig. 1, the average number of larvae per haul is shown.) The values that should be compared the number of individuals of S. ***buccaneeri*** per haul, their number as a percentage of all larvae obtained per haul and the lower limit of standard length. As can be seen from the table, they are very similar for these three samples, except for the number of individuals in C, and they reflect the homogeneous distribution of larvae throughout the oceanic region concerned, though the sampling area is separated into three lots. The high proportion of S. ***buccaneeri*** indicates the dominance of this species in all areas. In fact, the engraulid larvae in our samples seem to belong to exclusively S. ***buccaneeri.***

From the result of the collection by MTD horizontal closing net in the upper 500 m, which was carried out by Dr. Motoda and Mr. Kotori during the Hakuhō-maru cruise (Ocean Research Institute, 1970), the larvae seem to be limited in surface waters, the greatest depth of which is about 60 m. In the area of the Shunyō-maru cruise, sub-surface towing (20 to 30 m deep) was made simultaneously with surface towing under the same condition. The larvae of S. ***buccaneeri*** were caught more abundantly at the sub-surface than at the surface. The average number of individuals per haul and of the percentage number of larvae obtained per haul were 793.8 and 70.6 % respectively, while they were 440.7 and 59.2 % at surface towing (Table 2). The eggs could not be found in any samples of ours, though the eggs of MTD collections have not been examined yet.

(b) **Discussion**

As described above, we have found that the larvae of S. ***buccaneeri*** collected dominantly by larva net are distributed widely in the oceanic region of the Equatorial Western Pacific. Mr. K. Mori (personal communication) found at 2°49'N latitude and 141°11'E longitude, December, 1967, that shoals of S. ***buccaneeri*** were being pursued by yellowfin tuna, ***Thunnus*** *albacares*, and that the stomach of tuna or skipjack captured in the ocean was filled exclusively with these fishes. We may conclude that S. ***buccaneeri*** breeds and completes its life history in the oceanic waters concerned.

In the past, S. ***buccaneeri*** was reported mostly from neritic waters ranging all over the Indo-West Pacific region (Fig. 7) ; Indo-Australian Archipelago (Weber and De Beaufort, 1913—as ***zollingeri;*** Hardenberg, 1934—as ***zollingeri),*** Taiwan (Shen, 1959—as ***zollingeri),*** Hawaii (Strasburg, 1960), Japan (Hayashi and Tadokoro, 1962 a, b-as ***zollingeri),*** the Red Sea, Persian Gulf and Durban (Whitehead, 1965), Comoro Island (Whitehead, 1967 a), Malayan waters and Hong Kong (Whitehead, 1967 b), east of New Guinea (Far Seas Fisheries Research Laboratory, 1969 -as ***zollingeri),*** Philippine (Tiews ***et al.,*** 1970), etc.

Thus, the species occurs both in neritic and oceanic waters. These may be some connection between the two groups, i.e., they may originate from the same stocks. Such a connection can be investigated by comparing the meristic

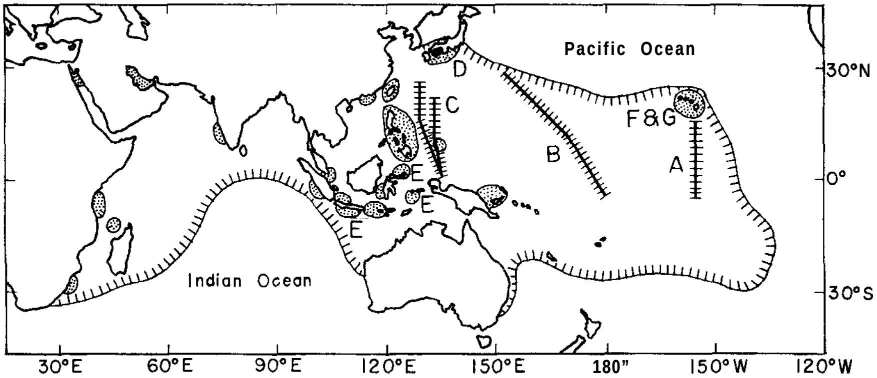

Fig. 7. Distribution of S. ***buccaneeri*** in the Indo-West Pacific region. Lines with two arms indicate the areas of present authors (see Fig. 1). Doted areas represent localities listed by Weber and De Beaufort (1913), Hardenberg (1934), Shen (1959), Strasburg (1960). Hayashi and Tadokoro (1962 a, b), Whitehead (1965, 1967 a, b), Far Seas Fisheries Research Laboratory (1969) and Tiews ***et al. (1970).*** Curves with a arm denote the boundary of Indo-West Pacific Fauna defined by Ekman (1953).

Table 3. Meristic counts of S. ***buccaneeri*** in 7 samples. Sources of data are as follows; A, B and C, larval sample of present authors ; D, Hayashi and Tadokoro (3.962 b) ; E, Hardenberg (1934) ; F, Strasburg (1960) ; G, Matsui (3.963). The letters A to G are illustrated in Fig. 7.

Area	Vertebrae			Dorsal fin rays			Anal fin rays		
	No. Sp.	x̄	s	No. Sp.	x̄	s	No. Sp.	x̄	s
A	54	42.481	0.574	53	13.377	0.527	54	14.852	0.627
B	29			24			25	34.830	0.723
D	87	42.586 42.471	0.501 0.607	84	13.583 13.452	0.504 0.547	85		
E	127 43	42.372 42.449	0.669 0.613	127	13.551	0.545	127	14.965 14.992	0.731 0.649
F	—		—	30	13.300	0.466	30	14.967	0.615
G	62	42.758	0.670	—	—	—	62	15.306	0.715

No. Sp. : Number of specimen. **x̄** : Average of counts.
s : Standard deviation.

counts among samples taken at different areas. In Table 3, counts of vertebrae including urostyle, and of dorsal and anal fin rays are shown. In the samples taken or quoted, the localities (illustrated in Fig. 7) are as follows; A from south of Hawaii, B from the area between Western Samoa and Japan, C from the area between southern Japan and north west of New Guinea, D from Japanese coastal waters (Hayashi and Tadokoro, 1962 b: Table 1), E from Puger, Ambon and Menado (Hardenberg, 1934 : Table 63), F from Hawaii (Strasburg, 1960 : Table 7) and G also from Hawaii (Matsui, 1963: Appendices 1 and 3). In A, B and C (our larval sample), larvae over 19 mm SL were selected, and were stained with alizarin-red solution (Itazawa, 1965) for counting meristic characters. It was known that one ray must be added to the anal fin ray count of Hayashi and Tadokoro (Dr. S. Hayashi, personal communication).

The average values for all counts are very similar and highly significant differences ($P \leq 0.01$) are not found as a result of t-test (Table 4) among 6 samples except for the Hawaiian one of Matsui, for which we have suggested previously that S. ***buccaneer-i*** might be partially confused with S. ***purpureus.*** In engraulid fishes, such as ***E. japonica*** (Asami, 1958; Takao, 1964) and S. ***purpureus*** (Tester and Hiatt, 1952; Matsui, 1963), meristic characters, especially vertebrae, show variations in number that form a useful method for analysis of local or seasonal races. S. ***buccaneeri*** may show similar variations in meristic counts. If such is the case, then the result of the t-test in Table 4 will support the assumption that two types of S. ***buccaneeri,*** i.e., a neritic and an oceanic type, may have connection with each other. In fact, the sporadic occurrence of ***S. buccaneeri*** in Japan (Hayashi and Tadokoro, 1962 a,b; Nakai ***et al.,*** 1969 — as ***zollingeri)*** and in Hawaii (Strasburg, 1960 ; Matsui, 1963) might be explained by immigration or transport by ocean currents into coastal waters from oceanic ones, bearing in mind the distribution of the larvae described above and the dominance of neritic engraulids, i. e., ***E. japonica*** in Japan and S. ***purpureus*** in Hawaii.

Table 4. Results of I-test among meristic counts of 7 samples in Table 3.

(1) Vertebrae

	B	C	D	E	G
A	—	—	—	—	+
B		—	—	—	—
C			—	—	++
D				—	++
E					++

(2) Anal fin rays (upper right) and dorsal fin rays (lower left)

	A	B	C	D	F	G
A						
B					—	+
C						++
D	+	—	—		—	++
F	—	+	—	+		+

— : Non significant. + : Significant at P-0.05.
++ : Significant at P=0.01.

From the descriptions above, it is possible to see some relationship between neritic and oceanic populations. A discrete neritic population, however, seems to occur in some areas (see p. 163). Since there is insufficient data, we can not discuss this problem in detail, being the subject for a future study.

We have found that the larvae of S. ***buccaneeri*** are distributed widely in surface waters all over the Equatorial Western Pacific. They made up 45 % or more of the larvae obtained in our samples. The species may play an ecological role as a forage fish, and therefore serve as a member of the vital link between the zooplankton and the larger predatory fishes, such as tuna, skipjack, etc.

VI. CONCLUSIONS

Larvae of S. ***buccaneeri,*** previously reported from only coastal waters, were caught mainly by larva net in the oceanic regions of the Equatorial Western Pacific. The life history of the species from early postlarva to adult is described in this paper. Compared with the fish taken in neritic waters, the oceanic samples show discrepancy in respect to the following characters : body proportions, the developmental sequence and the brain form. This variation, however, was considered to be intraspecific by the following seasons : the developmental stage may be variable depending on habitats and so the morphology of adults taken in various areas is not necessarily identical ; on S. ***buccaneeri,*** the larvae are distributed widely in the oceanic region, and it is assumed that the neritic populations may originate from the oceanic ones in some areas.

The intraspecific variations of developmental sequence was found to correlate with distribution. The oceanic ***buccaneer?*** has the following morphological characters: between 15 and 20 mm SL the postlarva rapidly changes its character, for example by a larger proportion of the head and denser pigmentation, and is transformed into a juvenile merely at about 25 mm SL; as a result of this sequence, the pigmy like adult (39.5 mm SL in this paper) has a very short pectoral-pelvic interspace ; and the brain of adult, perphaps retarded in its development, is well separated from the skull and has a typically slender telencephalon.

The larvae were collected dominantly, regardless of the ocean currents, and meristic counts did not show highly significant differences among 6 samples taken in different waters, It is concluded that S. ***buccaneer-i*** probably inhabits and completes its life history both in oceanic and neritic waters throughout the whole West Pacific region and further it is assumed that the sporadic occurrence of the species in Japan and Hawaii may follow the immigration into these neritic waters from oceanic ones.

Some aspects of the biology of S. ***buccaneeri*** have become clearer, and they seem to be somewhat peculiar among engraulids, which are neritic inhabitants. It must be noted, however, that several important points have been left unsolved ; the morphological variations corresponding to environmental conditions, the relation between the neritic and oceanic form and no collection of the eggs, etc. We hope more detail research will be carried out.

VII. ACKNOWLEDGEMENTS

This study was mainly conducted on the R/V Hakuho-maru Cruise KH-69-4. To Dr. R. Marumo (the chief scientist of the Cruise) of Ocean Research Institute, and to the officers and crews, we express our sincere gratitude for their help and cooperation. For the kind permission of the director and staffs of the ex-Nankai Regional Fisheries Research Laboratory, Fisheries Agency of Japan, the samples of the Shunyo-maru cruise were obtained by transfer to Fisheries Laboratory, Faculty of Agriculture, Kyushu University.

For the gift of the specimens, we wish to thank Dr. E. Nakamura of Bureau of Commercial Fisheries Research Laboratory, Honolulu, Mr. T. Kubota of Department of Fisheries, College of Marine Science and Technology, Tokai University, Mr. H. Ichikawa of Faculty of Fisheries, Kagoshima University, and Mr. K. Gushima of Faculty of Fisheries and Animal Husbandry, Hiroshima University.

We would like to thank Dr. S. Motoda and Mr. M. Kotori of Faculty of Fisheries, Hokkaido University for the gift of fish larvae in MTD collection. We are also indebted to Dr. S. Hayashi and Mr. K. Mori of Far Seas Fisheries Research Laboratory, for their kind information.

We are grateful to Dr. P. J. Whitehead of the British Museum (Natural History), London, for his critical reading of the manuscript and his kind information.

LITERATURE CITED

Ahlstrom, E. II. and R. C. Counts 1958 Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. Fish. *Bull. U. S. Wildl. Serv., 58 (139): 359-416*

Aikawa, H. 1961 *Zwashi no hanashi (Story of sardine).* Uchida Rokakuho, Tokyo, 169 pp., 24 figs., 27 tabs. (In Japanese)

Asami, T. 1958 On the patterns of development and growth of Japanese anchovy along the coast of Nankai and Naikai regions of Japan. *Rep. Nankai Reg. Fish. Res. Lab., (7)* : 1-*18.* (In Japanese with English summary)

Delsman, H. C. 1931 Fish eggs and larvae from the Java Sea. 17. The genus *Stolephorus. Treubia, 13 (2)* : *217-243*

Ekman, S. 1953 *Zoogeography of the Sea.* Sidgwick and Jackson Ltd, London. xiv-417 pp., 121 figs., 49 tabs.

Fage, L. 1940 Le plateau continental et la metamorphose des poissons. *Mém. Soc. Biogeogr., 7:* 23-29

Far Seas Fisheries Research Laboratory. 1969 *Shunyō-maru niyoru Bisumarukukai-Solomonkai gyogyochosa hōkoku (Report on the fisheries research in the Bismarck and the Solomon Seas by Shunyd-maru).* Fisheries Agency of Japan, Shimizu, ii+170 pp., 38 figs., 2 pls., 10 tabs., 1 app. tab. (In Japanese with English synopsis)

Fowler, H. W. 1941 Contributions to the biology of the Philippine Archipelago and adjacent regions. *Bull. U. S. Nat. Mus.,* 13 (100) : 1-879

Hardenberg, J. D. F. 1934 Some remarks on the genus *Stolephorus* Lacepede in the Indo-Australian Archipelago. *Treubia, 14 (3)* : 313-375

Hayashi, S. and A. Tadokoro 1962 a Occurrence of the *Taiwan-ainoko, Stolephorus rollingeri* (Bleeker), in Japan. *Bull. Jap.* Soc. *Sci. Fish., 28 (1) :* 26-29

—— *1962* b Catch of the *Taiwan'ainoko* in the anchovy fishing area around Japan. *Ibid.,* **28** *(1) : 30-33.* (In Japanese with English summary)

Itazawa, Y. 1958 On the number and modified forms of vertebrae found in the Japanese anchovy (*Engraulis japonicus*). *Ibid., 20 (7) : 591-598.* (In Japanese with English summary)

Kow, T. A. 1967 A contribution to the study of the growth of members of the genus *Stolephorus* Lacepede in Singapore Straits. *Proc. Zndo-Pacific Fish.* **Coun., 12** *(11): 1-25*

Matsui, T. 1963 *Population of anchovy baitfish* (Stolephorus) *in the vicinity of Maui, Hawaiian Islands.* Master of Science Thesis, Univ. of Hawaii, 99 pp., 12 figs., 6 apps.

Martin, W. R. 1949 The mechanics of environmental control of body form in fishes. *Univ. Toronto Studies, Biol. Ser.,* **58** : *5-72*

Munro, I. S. R. 1967 *The fishes of New Guinea.* Department of Agriculture, Stock and Fisheries, Port Moresby, New Guinea, xxxvii+651 pp., 84 pls., 23 figs.

Nakai, Z., T. Hirao and S. Kudoh 1969 A preliminary report on occurrence of *Stolephorus zollingeri* in Suruga Bay and the Sea of Enshu-nada in 1967 *Bull. Jap. Soc. Fish. Oceanogr., (15)* : 51-54 (In Japanese)

Nakai, Z., K. Honjo, K. Kidachi, H. Suzuki, T. Yokota, T. Tsujita, E. Ozasa, Y. Shojima and S. Nishimura 1962 *Zwashirui kōkishigyo no shokuji to kanyuryo tono kankei* (*Rela-*

tionships between food organisms and size of recruitment of iwashi). Suisan Sigen ni kansuru kyodo kenkyu suisin kaigi hōkokusho. Shown 36 nendo. Norin Suisan Gijutsu Kaigi, Tokyo. pp. 101-121 (In Japanese)

Nakamura, E. L. 1970 Synopsis of biological data on Hawaiian species of *Stolephorus. pp.* 425-446. In *"The Kuroshio" (A symposium of the Japan Current).* East-West Center Press, Honolulu

Ocean Research Institute 1970 *Preliminary report of the Hakuhō-maru Cruise KH-69-4 (IBP Cruise).* Univ. of Tokyo, Tokyo, 68 pp., 20 tabs., 17 figs.

Ogawa, Y. 1967 Morphological transition of the brain components of anchovy with their body-growth. *Bull. Jap.* Soc. *Sci. Fish., 33 (6)* : 531-538 (In Japanese with English summary)

Shen, S. 1959 Anchovies found in Taiwan. *Rep. Inst. Fish. Biol. Min. Eco. Aff. Nat. Taiwan Univ.,* **1** *(3) : 24-37*

Strasburg, D. W. 1960 A new Hawaiian engraulid fish. *Pac. Sci.,* 14 (4) : 395-399

Sverdrup, H. U., M. W. Johnson and R. H. Fleming 1967 *The Oceans* (Modern Asia Edition). Prentice-Hall, Englewood Cliffs, Charles E. Tuttle Company, Tokyo, x+ 1087 pp., 7 charts

Takao, K. 1964 Seto Naikai no katakuti-iwashi, *Engraulis japonica* (Houttuyn), no seitai ni tsuite (Ecological study on the Japanese anchovy, *Engraulis japonica* (Houttuyn), in the Seto Inland Sea). *Naikai Reg. Fish. Res. Lab., Publ. Ser. C, No. 2* (5), 50 *pp., 13* tabs., 8 figs., 1 app. tab.

Tester, A. L. and R. W. Hiatt 1952 Variation in the vertebral number of the anchovy *(Stolephorus purpureus)* in Hawaiian waters. *Pac. Sci., 6* (1) : 59-70

Thorson, G. 1961 Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. pp. 455-474. *In* "Oceanography" (Mary Sears, editor), The American Association for the advancement of Science, Publication No. 67, Washington, xi+654 pp.

Tiews, K., I. A. Ronquillo and L. M. Santos 1970 On the biology of anchovies *(Stolephorus* Lacepedej in Philippine waters. *Pro. Zndo-Pacific Fish. Coun., 13* (11) : 20-48

Uchida, K., S. Imai, S. Mito, S. Fujita, M. Ueno, Y. Shojima, T. Senta, M. Tafuku and Y. Dotsu 1958 *Studies on the eggs, larvae and juvenile of Japanese fishes. Ser. 1.* Kyushu Univ., Fukuoka, viii+88+10 pp., 86 pls. (In Japanese)

Uchihashi, K. 1953 Ecological study of Japanese teleosts in relation to the brain morphology. *Bull. Japan Sea Reg. Fish. Res. Lab., (2) : l-166* (In Japanese)

Uda, M. and K. Hasunuma 1969 The eastward subtropical countercurrent in the western North Pacific Ocean. *Jour. Oceanogr. Soc. Japan, 25 (4) : XI-210*

Weber, M. and L. F. De Beaufort 1913 *The fishes of the Zndo-Australian Archipelago. 2.* E. J. Brill, Leiden, xiii-j-404 pp., 151 figs.

Whitehead, P. J. P. 1965 A review of the elopoid and clupeoid flshes of the Red Sea and adjacent regions. *Bull, Br. Mus. nat. Hist. (Zool.), 12 (7)* : 225-281

Whitehead, P. J. P., M. Boeseman and A. C. Wheeler 1966 The types of Bleeker's Indo-Pacific elopoid and clupeoid fishes. *Zool. Verhandl, Leiden,* (84) : l-159

—— 1967 a Indian Ocean anchovies collected by the *Anton Brunn and Te Vega,* 1963-64. *J. Mar. biol. Ass. India, 9 (1) : 13-37*

—— *1967* b The clupeoid fishes of Malaya. *Ibid., 9 (2) : 223-280*

Yamashita, D. T. 3951 *The embryological and larval development of the nehu, an engraulid baitfish of the Hawaiian Islands.* Master of Science Thesis, Univ. of Hawaii. 61 pp., 12 pls., 7 figs.