Seasonal Differences in Spawning, Egg Size, and Early Development Time of the Hawaiian Anchovy or Nehu, *Encrasicholina purpurea*[1]

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ABSTRACT: **Nehu spawning is concentrated in a 1 hour period shortly after sunset; the delay after sunset is longer in the winter than in summer. Incubation time for nehu eggs is 22–35 hours and is inversely related to temperature. Development time between hatching and first feeding shows relatively greater seasonal differences, and total embryonic development time during the coldest months is almost twice that of the warmest months. Nehu egg size is inversely related to temperature. The seasonal differences in egg size are probably the result of a physiological response to temperature. The potential adaptive value of the seasonal change in egg size in this tropical species is more likely related to size-specific differences in predation rates rather than to seasonal changes in abundance or size of food for larvae. The seasonal changes in total development time result in marked differences in the time of the diel cycle at which larvae reach first-feeding status; these differences could have more influence on survival of small larvae than effects related to either predation or food availability.**

Seasonal differences in egg size, incubation, and posthatch embryonic development time have been reported for many species of temperate or higher latitude fishes. Some reports, e.g., Blaxter and Hempel (1963), involve differences between stocks or populations with different spawning seasons. Other examples, e.g., Ware (1977), deal with differences occurring over the spawning season of an apparent single stock. Hypotheses presented about the potential mechanisms or adaptive significance of seasonal differences are related to the rather marked seasonal changes in temperature, productivity, etc., that are typical of high latitude environments. Seasonal differences in egg size and early development have not been investigated in fishes from tropical latitudes where seasonal environmental changes are less extreme than at higher latitudes.

The Hawaiian anchovy or nehu, *Encrasicholina purpurea*, spawns throughout the year in enclosed, semiestuarine areas of Hawaii (Tester, 1955; Clarke 1987). Preliminary studies indicated that spawning occurs over a very short period after dusk. Because of this, it was possible not only to obtain freshly spawned eggs readily, but also to identify "day-classes" of eggs and prefeeding larvae throughout the diel cycle and thus to estimate incubation and development times from field samples. This paper reports on seasonal differences in spawning, egg size and development and considers hypotheses based on studies from higher latitudes in the context of seasonal environmental changes in the tropics.

MATERIALS AND METHODS

All material was collected from Kaneohe Bay, a semienclosed basin on the northeast side of the island of Oahu, HI. Plankton samples were collected with a 1 m diameter, 5 m long conical plankton net of 0.335 mm mesh. The net was rigged with a three-point bridle to which a ca. 3 kg weight was attached. The net was simply dropped mouth downward, allowed to fish to the bottom (12–15 m), and retrieved by a tether attached to a choke line about 1 m behind the mouth. The sample was immediatly preserved in a ca. 4% formaldehyde/seawater solution. The present study was conducted during the course of a long-term survey of nehu egg abundance that sampled stations throughout Kaneohe Bay between the hours of 0600 and 1100 at approximately weekly intervals. These samples provided eggs and larvae from the morning hours and also indicated periods and locations of high egg or larval abundance for sampling at other times of the day.

Previous studies (Clarke 1987) on adult female nehu indicated that spawning occurs during a short period (a few hours) after sunset. In order to determine spawning time more precisely, plankton samples were taken at hourly intervals between sunset and midnight at four different times of the year. Based on data from the most

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recent regular egg survey, one to three stations were sampled close to the solstices and equinoxes: 30 September 1984; 27 December 1984; 21 March 1985; and 26 June 1985. The hours sampled also included expected hatching time for the previous night's eggs for all dates except March, in which case samples were also taken at 0300–0430. The stations were also sampled in the afternoon, 1–2 days after the sunset to midnight series. Times of sunset and sunrise for the above dates were taken from astronomical tables. Water temperatures for each period were taken from the data log at the Hawaii Institute of Marine Biology laboratory at Coconut Island. Hourly surface temperatures for a 2 wk period bracketing the sampling were averaged.

Nehu eggs and larvae are easily identified. Eggs were usually very numerous (100's per sample) and were either all at very nearly the same stage or, for certain times of the day in December and March, readily separated into two age groups: eggs from the most recent spawning and much more developed eggs from the previous night's spawning. There were many fewer larvae in the samples (typically 10's per sample); in several cases larvae from 2 to 4 different samples taken within an hour of each other were combined in order to assess development at a given time of day. Larvae less than 4 mm notochord length could be separated into either two or three age groups based primarily upon presence or absence of yolk, pectoral fins and rays, and eye pigmentation. Between appearance of the pectoral fin buds and development of pectoral rays, age groups could be further discriminated using the diameter of the roughly semicircular pectoral fin bases relative to that of the pupil or the orbit (neither of which appeared to increase significantly after the pectoral buds appear). Other characters such as the development of the mouth or the gut were correlated with the principal characters used, but were not as useful for qualitative separation. For any given time of day, the least developed larvae were considered "0" group larvae (0–24 h past hatching); the next most developed, "1" group (24–48 h past hatching); and the third, if present, "2" group (48–72 h past hatching).

Except for the late afternoon samples from June, there was no difficulty in separating small larvae into age/development groups, i.e., larvae in each of the two or three groups present were similar to each other and there were no intermediates. In the June series, the apparent oldest group of afternoon larvae showed a broader range of several features than was evident for similar stages at other seasons. There was, however, still no overlap with younger stages, and after examination of more larvae from other afternoon samples taken at the same time of the year in 1984 and 1985, it was concluded that these larvae represented only one variably developed age group (see Results section). Larvae larger than 4 mm notochord length were taken infrequently, and it was not possible to estimate age groups among these on the basis of either size of development.

Volumes and dry weights were determined for undamaged newly spawned eggs from each season. Nehu eggs are ellipsoidal with the major axis about twice the minor. The yolk mass is similarly shaped and separated from the chorion by an obvious pervitelline space. For 40–50 freshly spawned eggs from each season (except June when only 29 eggs with no visible embryo were available), the major and minor diameters of both the entire egg and the yolk within were measured to the nearest 0.01 mm using an ocular micrometer at 100× magnification. Egg and yolk volumes were calculated using the formula for a prolate spheroid. Replicate samples (3 per season) of 20 eggs each were rinsed with distilled water, placed in a preweighed aluminum pan and dried at 60°C. Weights of empty and full pans were determined to the nearest 0.002 mg; weight per egg was calculated by subtraction and division by the number of eggs in the sample.

Dry weights were also determined for samples of 10–20 hydrated ovarian ova from spawning nehu taken by purse seine. Preliminary studies indicated that unless ova had already ovulated, they could not be reliably and completely separated from follicular tissue. The time between ovulation and spawning is apparently very short (Clarke 1987), and few samples of adult nehu contained many fish in this condition. Consequently, the only data reported here were from 10 females taken from a purse seine collection on 1 June 1983. This collection contained the widest size range (39–61 mm SL) of females with ova free in the oviducts.

Notochord lengths of larvae were measured to the nearest 0.1 mm. There were, however, usually less than 10 larvae of each day class at each different time of day, and statistical comparisons of average length between seasons for the same stages were not possible. The numbers of undamaged larvae suitable for dry weight determinations were even lower. Dry weight determinations were made for only three samples

of 5–10 larvae each from September and six samples of 10 each from March.

RESULTS

Spawning

The dusk-to-midnight samples from all four seasons clearly indicated that spawning was concentrated within a ca. 1 h period shortly after sunset. Newly spawned eggs, with no evidence of embryonic development under low magnification, were absent from initial samples and appeared in large numbers in samples 1.5–3 hours after sunset. The eggs in samples taken ca. 1 hour after first appearance of new eggs were already either mostly or totally in early cleavage stages. In the June series, many of the new eggs in the first sample containing new eggs were already in early cleaveage stages. Newly spawned eggs were very rare in samples taken ca. 1 hour after first appearance and were absent from later samples. Thus spawning appears to be concentrated within a period of 1 hour or less. The estimated midpoints of spawning time (Table 1) indicate that spawning occurs about 3 hours earlier in winter than in summer. The difference is not entirely accounted for by the earlier sunset in the winter months; the delay after sunset is less than in summer. These estimates of seasonal changes in spawning time agree with trends evident from mature females (Clarke 1987).

Incubation

In June and September, the incubation period was less than a day, and two day classes of eggs never occurred in the same sample. By early morning, embryos already extended about halfway around the remaining yolk. By late afternoon they extended over three-fourths of the way around the yolk, and the tail had flexed sideways. In both months the eggs apparently hatched about 22 hours after spawning time. During a 1 h period the "old " eggs disappeared, and newly hatched larvae appeared.

Incubation time was considerably longer in December and March. Eggs taken in the morning and afternoon were noticeably less developed than those from the same times in June or September. Both "old" eggs and recently spawned eggs were present between spawning time and midnight in December. No "old" eggs were present in any morning samples, and the embryos in the latest (2400 h) night samples appeared almost ready to hatch, judged from comparable stages in the June and September samples. Thus

TABLE 1.—Summary of data on spawning time, duration of egg and prefeeding larval stages, and egg size of the Hawaiian anchovy, *Encrasicholina purpurea*, in September and December 1984 and March and June 1985. Times of sunrise, sunset, spawning, and hatching are Hawaiian Standard Time. Temperature values are the means and ranges of hourly surface temperatures for a 2 wk period bracketing the sampling dates (see text). Values for egg and yolk volume are means and standard deviations of volumes calculated from length and width measurements.

	Sept.	Dec.	Mar.	June
Sunset	1800	1730	1800	1900
Sunrise	0600	0645	0600	0515
Spawning	2100	1900	2000	2200
Hatching	1900	0100	0700	2000
Temp. (°C)	27.7	23.1	22.2	26.5
(range)	(27.4-28.1)	(22.5-23.9)	(21.6-23.1)	(25.9-27.1)
Incubation (h)	22	30	35	22
Hatch-feeding (h)	35	54	71	47-57
Total (h)	57	84	106	69-79
Egg weight (g)	14.8	17.9	19.5	14.9
Egg vol. (mm^3)	0.195	0.248	0.262	0.211
(SD)	(0.023)	(0.024)	(0.019)	(0.016)
Yolk vol. (mm^3)	0.168	0.204	0.222	0.166
(SD)	(0.020)	(0.025)	(0.022)	(0.017)

hatching time was probably about 0100 and total incubation time about 30 hours. In March, old eggs were present along with new eggs between spawning time and 0430, but were absent from the earliest postsunrise sample taken at 0820. Old eggs were, however, present in samples taken at 0600–0700 earlier in March; this indicates that hatching time was probably about 0700 and that incubation time was about 35 hours.

Early Development

Development to first feeding status was most rapid in September (Table 2). By the end of the first day, the yolk sac had disappeared, and the pectoral fin bases were almost the same diameter as the eye. By the morning of the second day, the "1" larvae had black eyes and pectoral fins with well-developed rays; most individuals had food items in the gut. Similar larvae occurred in samples taken nearer to sunrise on other dates in September–October. Thus it is likely that the "1" larvae were ready to feed at or near sunrise and that development time from hatching to first feeding was about 35 hours (Table 1).

Development was considerably slower in December and March (Table 2). Some yolk remained at the end of the first day in both months. In December, "2" larvae had already been feeding by 0800 and probably reached feeding status at or near sunrise or about 54 hours after hatching. In March, early "3" larvae taken at 0845 had already been feeding, and the late "2" larvae appeared to have reached feeding status at or just before sunrise, about 71 hours after hatching.

In June the larvae developed almost as fast during the first day as in September (Table 2), but little change took place over the second night. In the morning only a few of the "1" larvae had traces of eye pigment. By afternoon there was a relatively wide range of development among apparent "1" larvae; they had white to brown eyes and variably developed pectoral rays. The mouths of some individuals appeared

TABLE 2.—Developmental characters of different age groups of early larvae of the Hawaiian anchovy, *Encrasicholina purpurea*, at different times of the day for four different sampling dates. Codes for yolk sac (Y) are: + = present along ventral margin, T = traces anteriorly, 0 = absent; for pectoral fin; 0 = absent, B = buds visible, P = diameter of bases about equal to that of eye pupil, E = bases diameter about equal to that of eye, and R = fin rays visible; for eye pigment (E): 0 = none, T = trace, Br = brownish, Bl = black, fully pigmented. Very early stages, which would otherwise be coded "+-0-0", are coded as "NH" or "STR" depending upon whether the larvae were newly hatched and still bent anteriorly or had straightened, respectively. Larvae apparently developed to feeding status, which would otherwise be coded "O-R-Bl", are simply designated by "F".

Date / Time	Age group: Character:	"0" Y–P–E	"1" Y–P–E	"2" Y–P–E
September 1984				
1900		NH	O-E-O	
2200-2300		STR	O-E-T	
1030		T-B-O	F	
1600		O-P-O	F	
December 1984				
0800		NH	T-P-O	F
1830		STR	O-E-O	F
2330		T-O-O	O-E-T	F
March 1985				
0830		NH	T-B-O	O-E-T
1500		STR	O-P-O	O-E-?
2030-2330		+–O–W	O–E–O	O–E–Br/Bl
0330–0430		+–B–O	O–E–T	O–R–Bl
June 1985				
2100–2200		NH	O–B–O	F
0800–0900		T–B–O	O–E–O/T	F
1400–1800		O–P–O	O–R–O/Br	F

nearly fully developed. In the night samples, all early "2" larvae appeared developed to feeding stage and some had traces of food in the gut; "2" larvae in morning samples were feeding. Thus some of the June larvae may have reached feeding status just before sunset or ca. 47 hours since hatching, but many apparently did not develop to this point until after dark and did not start feeding until the next morning or about 57 hours since hatching (Table 1).

Egg Size

Dry weight and volume estimates indicated that egg size was about the same in September and June, but ca. 25% and 30% larger in December and March, respectively (Table 1). The ratios (Sept.:Dec.:Mar.:June) of estimated dry weight per egg were 1:1:21:1.32:1.01. Similar ratios for average yolk volume (1:1.21:1.32:0.99) were closer to those for weights than were the ratios for whole egg volume (1:1.27:1.34:1.08). Yolk volume averaged 79–86% of whole egg volume with no evidence of a trend with egg size. The ratios of egg to yolk for both width and length ranged between 1.05 and 1.09. Except for a value of 2.07 for March yolk length to width ratio, the other length to width ratios for both egg and yolk ranged from 2.16 to 2.26.

Available data on larval size are few, but indicate a positive relationship with egg size. In all months, the newly hatched larvae were about the same length (2.0–2.2 mm), but larvae at or near first feeding status were 3.0–3.7 mm long in March and December as opposed to 2.8–3.0 mm in September and 3.0–3.5 mm in June. Mean dry weights of late "0" and early "1" larvae from September and March were 63% and 65%, respectively, of mean egg weights for the same periods, indicating commensurately heavier larvae from the larger March eggs.

The average weight per egg of hydrated ova taken from 10 females 39–61 mm standard length was 17.8 μg. The estimates from different individuals ranged between 14.4 and 19.2 μg/egg. The value for the smallest female was well below that of the other nine (42.5–61 mm SL); the next lowest value was 16.3 μg/egg. There was, however, no correlation between average weight per egg and female length for the whole series ($P > 0.20$, Spearman rank correlation coefficient).

Discussion

The observed seasonal differences in nehu reproductive parameters are not likely owing to genetic differences between seasonal subpopulations. Nehu reach spawning size at an age of 3–4 months and rarely live as long as six months (Struhsaker and Uchiyama 1976). Thus the progeny of, e.g., March spawners would be spawning in July–September rather than the following March. Although annual changes in environmental factors in Hawaii are fewer than at higher latitudes, nehu spawn throughout the entire year rather than over a short season, and the observed differences in spawning time, egg size, etc., are most likely responses to changes in temperature, day length, light levels, etc., encountered over the entire annual cycle.

The movement of adult nehu to spawning areas and their near synchronous release of eggs are probably stimulated by decreasing light levels in the afternoon and evening, but the timing is not simply related to seasonal changes in day length and time of sunset. The delay between sunset and spawning was less in the winter, possibly because light levels in the water column decrease earlier, relative to sunset, in the winter than in the summer owing to differences in solar elevation. It is also possible that responses to light are modified by some other seasonal factor, e.g., temperature.

Seasonal changes in egg size have been reported from apparently the same stock for many other species of fishes. For example, Ware's (1977) data on egg diameters of *Scomber scombrus* in the Gulf of St. Lawrence indicate that egg volume at the beginning of the spawning season (early June) is about twice that at the end (mid-August). The central population of the northern anchovy, *Engraulis mordax*, is more similar to nehu in that it spawns year round, and maximum egg volume, which occurs in March, is about 20% greater than the minimum in September–October (Hunter and Leong 1981).

Several mechanisms for within-stock, seasonal changes in egg size have been suggested. Egg size may be related to size of the spawning females, and the seasonal trend in egg size due to the larger females' spawning early in the season and the smaller ones later (Bagenal 1971). The data on ovarian egg weights from spawning nehu indicate no relation between egg size and female size; furthermore, there is no evidence of seasonal changes in size composition of spawning nehu. Clarke (1987) found no difference in size composition between winter and summer spawners examined for fecundity; unpublished data from that study show that size composition of

spawning nehu fluctuates throughout the year, but that there is no tendency for e.g., March spawners to be larger (or smaller) than September spawners. Egg size has been shown to be both positively and negatively affected by food supply or ration (Bagenal 1969; Hislop et al. 1978). The abundance of macrozooplankton, upon which adult nehu feed, does not appear to change systematically with season in Kaneohe Bay (Hirota and Szyper 1976). Daily ration or the fraction available for reproduction could, however, change seasonally due to differences in temperature or day length, but relevant studies to consider this possibility have not been done.

Imai and Tanaka (1987) demonstrated that egg size of *Engraulis japonica* responds more directly to temperature changes, and several potential mechanisms have been proposed. Daoulas and Economou (1986) suggested that egg size would be inversely correlated with temperature if oocyte differentiation rates increased relative to oocyte growth rates with increasing temperature. Tanasichuk and Ware (1987) hypothesized that gonadotropin secretion rates increase with temperature and cause a decrease in preovulatory atresia. For a given effort per batch, this would result in more, but smaller eggs at ovulation. Nehu fecundity is higher in the summer when egg size is lowest, and the increase in the summer is only partly accounted for by higher effort per batch (Clarke 1987). If effort per batch is controlled by some other factor, either of the above hypotheses could apply to nehu.

Several studies have hypothesized that both within- and between-stock differences in egg size are adaptive and related to minimizing mortality owing to starvation of early larvae. Blaxter and Hempel (1963) showed that larvae from large herring eggs were probably better able to survive situations with low food abundance. Ware (1977) showed that egg size in *Scomber scombrus* was positively correlated with the size of food items available for newly hatched larvae. There is, however, no evidence that nehu larvae encounter marked seasonal changes in food abundance or size. Kaneohe Bay is highly productive all year; Hirota and Szyper (1976) found no seasonal trends in total microzooplankton abundance. My own unpublished data indicate that concentrations and sizes of small copepod nauplii, the dominant prey of first-feeding nehu larvae (Burdick 1969), are similar throughout the year.

Ware (1975) and Tanasichuk and Ware (1987) have shown that a mechanism resulting in a decrease in egg size with increasing temperature would be selectively advantageous if egg and larval mortality rates were inversely related to egg size and if incubation times were inversely related to temperature (and not to egg size). Small nehu eggs and larvae would probably be subject to higher mortality owing to predation than would larger eggs and larvae at all times of the year, regardless of the apparent lack of variability in larval food supply. Furthermore, Yamashita's (1951) results indicate that differences in incubation time are caused by temperature and not egg size. Yamashita incubated nehu eggs from a single sample from Kaneohe Bay at different temperatures. Allowing for the fact that all his eggs had already spent a few hours at ambient temperature, the change in incubation time with temperature was similar to that evident from the seasonal data of the present study. Similar studies on other engraulids (King et al. 1978; Lasker 1964) have also shown negative correlations between incubation time and temperature that were presumably independent of egg size. Thus Ware's (1975) basic assumptions and hypothesis about factors selecting for egg size-temperature relationships seem to be applicable to nehu.

The duration of the period between hatching and first feeding (HF) was also negatively correlated with temperature. There were, however, seasonal differences in the ratio of posthatch to prehatch embryonic development time. HF was 1.60, 1.78, 2.02, and 2.14 times incubation time for September, December, March, and June, respectively (using HF = 47 hours for June). This indicates either that the effects of temperature on HF are qualitatively different from those on incubation, or that some other factor also affects posthatch development rate. For a range of temperatures that included those observed in this study, Houde (1974) showed that increasing temperature caused decreases in the period between hatching and eye pigmentation of larval *Anchoa mitchelli*. To the extent that seasonal differences in HF of nehu are similarly caused by temperature differences, this would tend to augment any selective advantage for larger eggs and larvae during the winter.

Even though Ware's (1975) hypothesis could potentially apply to nehu, the point in the diel cycle at which larval feeding becomes possible could have more important consequences to larval survival than differences in either egg size or

total development time. Small nehu larvae feed only during the day (Burdick 1969; Johnson 1982). In September, December, and March, larvae reached first-feeding status at or shortly before sunrise, could begin feeding as soon as they were able, and had an entire day to feed before having to survive the next night. In June, however, the larvae reached first-feeding status near sunset, had little or no chance to feed, and had to survive the night mostly or solely on internal reserves. Nehu larvae would face situations similar to June whenever the total time from spawning to first-feeding status was close to a multiple of 24 hours. (Other such periods would have occurred between September and December, between December and March, and between March and June.) If larvae during such periods had exhausted their internal reserves before they had a chance to feed, survivorship could have been greatly reduced compared with periods when larvae reached first-feeding status near dawn.

The time between reaching first-feeding status and irreversible starvation of nehu larvae is not known. It is usually of the order of days for fishes from higher latitudes (Hunter 1981), but is probably considerably less for nehu given that their incubation and development times are much shorter than those of most higher latitude species. Houde (1974) found that survival and growth of larvae of *Anchoa mitchelli* at 22°–28°C was unaffected by delaying feeding up to 24 hours or more after development of eye pigmentation, but nehu may be less tolerant. The development time between hatching and feeding status is longer for nehu than for *A. mitchelli* at similar temperatures, and visible yolk is gone at an earlier stage in nehu.

The seasonal changes in total time between spawning and reaching first-feeding status thus could result in fluctuations of mortality rates of nehu larvae throughout the year independent of either food supply or predation rates. Such fluctuations would not be expected in species from higher latitudes because differences of a few hours between reaching first-feeding status and the opportunity to feed are probably not as critical. Furthermore, spawning in many species, e.g., the northern anchovy, *Engraulis mordax*, is not as synchronous as in nehu and is spread over a broader portion of the diel cycle (Hunter and Macewicz 1980). Consequently, larvae from a given day's cohort would reach first-feeding status at various points during the diel cycle regardless of the absolute duration of the period between spawning and HF status.

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LITERATURE CITED

Bagenal, T. B.
1969. The relationship between food supply and fecundity in brown trout *Salmo trutta*. J. Fish Biol. 1:167–182.
1971. The inter-relation of the size of fish eggs, the date of spawning, and the production cycle. J. Fish Biol. 3:207–219.

Blaxter, J. H. S., and G. Hempel.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. perm. int. Explor. Mer 28:211–240.

Burdick, J.
1969. The feeding habits of nehu (Hawaiian anchovy) larvae. M.S. Thesis, Univ. Hawaii, Honolulu, 54 p.

Clarke, T. A.
1987. Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 85:127–138.

Daoulas, C., and A. N. Economou.
1986. Seasonal variation of egg size in the sardine, *Sardina pilchardus* Walb., of the Saronikos Gulf: causes and a probable explanation. J. Fish Biol. 28:449–457.

Hirota, J., and J. P. Szyper.
1976. Standing stocks of zooplankton size-classes and trophic levels in Kaneohe Bay, Oahu, Hawaiian Islands. Pac. Sci. 30:342–361.

Hislop, J. R. G., A. P. Robb, and J. A. Gauld.
1978. Observations on effects of feeding level on growth and reproduction in hadduck, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish Biol. 13:85–98.

Houde, E. D.
1974. Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical marine fishes. Mar. Biol. (N.Y.) 26:271–285.

Hunter, J. R.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae, morphology, ecology, and relation to fisheries, p. 34–77. Univ. Washington Press, Seattle, WA.

Hunter, J. R., and R. Leong.
1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215–230.

Hunter, J. R., and B. J. Macewicz.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Fish. Invest. Rep. 21:139–149.

Imai, C., and S. Tanaka.
1987. Effect of sea water temperature on egg size of Japanese anchovy. Nippon Suisan Gakkaishi 53:2169–2178.

Johnson, L. R.
1982. Feeding chronology and daily ration of first-feeding larval Hawaiian anchovy, *Stolephorus purpureus*. M.S. Thesis, Univ. Hawaii, Honolulu 78 p.

King, D. P. F., A. A. Robertson, and P. A. Shelton.
1978. Laboratory observations on the early development of the anchovy *Engraulis capensis* from the Cape Peninsula. Fish. Bull. S. Afr. 10:37–45.

Lasker, R.
1964. An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. Copeia 1964:399–405.

Struhsaker, P. J., and J. H. Uchiyama.
1976. Age and growth of the nehu, *Stoleahorus purpureus* (Pisces:Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9–17.

Tanasichuk, R. W., and D. M. Ware.
1987. Influence of interannual variations in winter sea temperature on fecundity and egg size in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 44:1485–1895.

Testor, A. L.
1955. Variation in egg and larva production of the anchovy, *Stolephorus purpureus* Fowler, in Kaneohe Bay, Oahu, during 1950–1952. Pac. Sci. 9:31–41.

Ware, D. M.
1977. Spawning time and egg size of Atlantic mackerel, *Scomber scombrus*, in relation to the plankton. J. Fish. Res. Board Can. 34:2308–2315.
1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32:2503–2512.

Yamashita, D. T.
1951. The embryological and larval development of the nehu, an engraulid baitfish of the Hawaiian Islands. M.S. Thesis, Univ. Hawaii, Honolulu, 64 p.