

AN INVERSE CORRELATION BETWEEN MERISTIC CHARACTERS AND FOOD SUPPLY IN MID-WATER FISHES: EVIDENCE AND POSSIBLE EXPLANATIONS

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ABSTRACT

In five species of mid-water fishes, *Chauliodus sloani*, *Diplophos taenia*, *Pollichthys maui*, *Vinciguerrria lucetia*, and *V. nimbaria*, the central values of meristic counts (anal fin rays, vertebrae, longitudinal photophore rows) and three measures of biological productivity (phosphate-phosphorus concentration, net primary production, zooplankton standing stocks) are correlated negatively. For the species and areas studied the meristic variation observed cannot be related to temperature, salinity, dissolved oxygen, or any other physical or chemical factor known to affect meristic variation in fishes. It is hypothesized that this relationship between meristic counts and measures of food availability involves differences in egg size, fecundity, size at hatching, and size at comparable stages of larval development between populations in different areas, and that these differences in turn reflect adaptations to low food densities in areas of low productivity and higher predator densities in areas of higher productivity.

Meristic characters have been widely used in studies of fish populations and species. Unlike body proportions or coloration, meristic characters are fixed usually at or before metamorphosis and remain constant throughout the life of an individual. Variation in meristic characters stems from both genetic variation between populations and species, and from environmental variation, which, within genetically controlled limits, can directly affect the number of parts formed in developing embryos and larvae. Recent reviews of factors known to affect meristic characters in fishes include Barlow (1961), Blaxter (1969), Gar-side (1966), and Fowler (1970).

An inverse relationship between vertebral and/or other meristic counts and water temperature at the time of early development has been demonstrated in numerous studies (see above review articles). Experimental studies have shown that in many cases the effect of temperature upon meristic characters occurs within a restricted period of time, the so-called sensitive period, and that variations in temperature before and after this period have no effect (Hempel and Blaxter 1961). The sensitive period may vary with

different structures with the result that the timing, magnitude, and in some cases the direction of response of different structures to temperature variation differs among different species (Fowler 1970).

Hubbs (1926), Barlow (1961), and others, have suggested that the relationship between meristic counts and temperature involves differential effects of temperature on rate of growth versus rate of differentiation, with the result that accelerated growth is associated with a shortening of the sensitive period, resulting in the laying down of fewer parts. The conclusion is that conditions retarding growth rates are associated with elevated meristic counts, conditions accelerating growth rates are associated with lowered meristic counts. This explanation has been extended to factors other than temperature known to affect meristic characters in fishes: dissolved oxygen concentration (Alderdice et al. 1958), salinity (Forrester and Alderdice 1966; Blackburn 1967), carbon dioxide concentration, light intensity, exposure to X-rays, etc. (see Fowler 1970).

In 1972, we reported a significant negative correlation between certain meristic counts in *Diplophos taenia* and three measures of food supply: net primary production, phosphate-phosphorus concentration, and zooplankton standing stocks (Johnson and Barnett 1972). To our knowledge, this was the first suggestion of a

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possible relationship between meristic counts and measures of food supply. We did not offer any explanation for this relationship in the earlier report. In the present paper we extend our information on *D. taenia* to the Atlantic Ocean, present corroborative evidence for the relationship between meristic counts and food supply based on four other species of mid-water fishes, and attempt to show that the relationship for the species and areas studied is with food supply and not temperature, salinity, or dissolved oxygen. We hypothesize that this relationship between meristic counts and food supply reflects differences in egg size, fecundity, size at hatching, and size at comparable stages of larval development between populations in different areas, and that these differences represent adaptations to low food densities in areas of low productivity and higher predator densities in areas of higher productivity.

METHODS

Collection and Analysis of Data

Methods of taking counts follow those of Grey (1964), Morrow (1964), and Johnson (1970). Photophore rows in a generalized stomiatoid fish are illustrated in Morrow (1964: Figure 73), but our nomenclature for segments of photophore rows follows that of Johnson (1970). All vertebral centra were counted including the compound element supporting the parhypural and hypurals (Weitzman 1967). Standard statistical texts have been used as reference material (especially Tate and Clelland 1957; Sokal and Rohlf 1969). Agreement between sets of ranks is assessed via the tau coefficient of correlation or Kendall's coefficient of concordance, W (see Tate and Clelland 1957).

Localities Studied

We have studied specimens from eight areas (Figure 1): 1) the eastern tropical Pacific (ETP) off Mexico; 2) the central North Pacific (CNP) off the Hawaiian Islands; 3) the central equatorial Pacific (CEP) at long. 145° to 150°W; 4) the western equatorial Pacific (WEP) around long. 170°E; 5) the Philippine Sea (PS); 6) the South China Sea (SCS); 7) the Gulf of Guinea (GG); and 8) the central North Atlantic (CNA) including the Sargasso Sea. All of these areas are tropical oceanic habitats and represent a wide range of physical and biological features.

Measures of Biological Productivity

The measures used to assess relative richness of food supply are phosphate-phosphorus concentration, net primary production, and zooplankton standing stocks. These three variables are highly intercorrelated (Cushing 1971). These measures were chosen because there are published attempts at contouring values of these variables on an oceanwide basis and because values for them are commonly reported in more regionally oriented studies.

Despite many problems in both sampling and interpretation associated with attempts to contour values of biological variables on an oceanwide basis and to integrate values based on a limited number of measurements over a full year, we were forced to accept such attempts as the principal basis for ranking our eight study areas with respect to the three measures of food supply. Where possible we relied on synoptic studies presenting contours on an oceanwide basis: net primary production (as mg-C/m² per day, Koblentz-Mishke et al. 1970; as g-C/m² per year, Ebeling 1962 based on Fleming and Laevastu 1956), zooplankton concentration (as parts/10⁶ by volume in the upper 150 m of the Pacific Ocean, Reid 1962), and phosphate-phosphorus concentration (as μg-at/liter contoured at 100 m in the Pacific Ocean, Reid 1962). Where these studies did not cover several of our study areas, we used regional studies (SCS: Angot, Steemann Nielsen in Wyrski 1961; Sorokin 1973; GG: Raymont 1963, Corcoran and Mahnken 1969, Kinzer 1969, Zeitschel 1969, Riley 1972; CNA: Menzel and Ryther 1961, Raymont 1963, Corcoran and Mahnken 1969, Zeitschel 1969, Riley 1972).

We compared the contours or values for each of the three measures of productivity over all eight study areas and then ranked the eight areas with respect to each other for each measure (Table 1). As expected (Cushing 1971), the ranks for the three measures over the eight areas are highly concordant ($W_{3,8} = 0.85$, $P < 0.01$, concordance coefficient corrected for ties, see Tate and Clelland 1957). This highly significant concordance increases our confidence in this approach to ranking the eight areas with respect to productivity and allows summation of the ranks of the three measures of food supply over each area, yielding a rank-sum. We then ranked this rank-sum and obtained the following rank-index order of productivity, from highest to lowest: 1) eastern

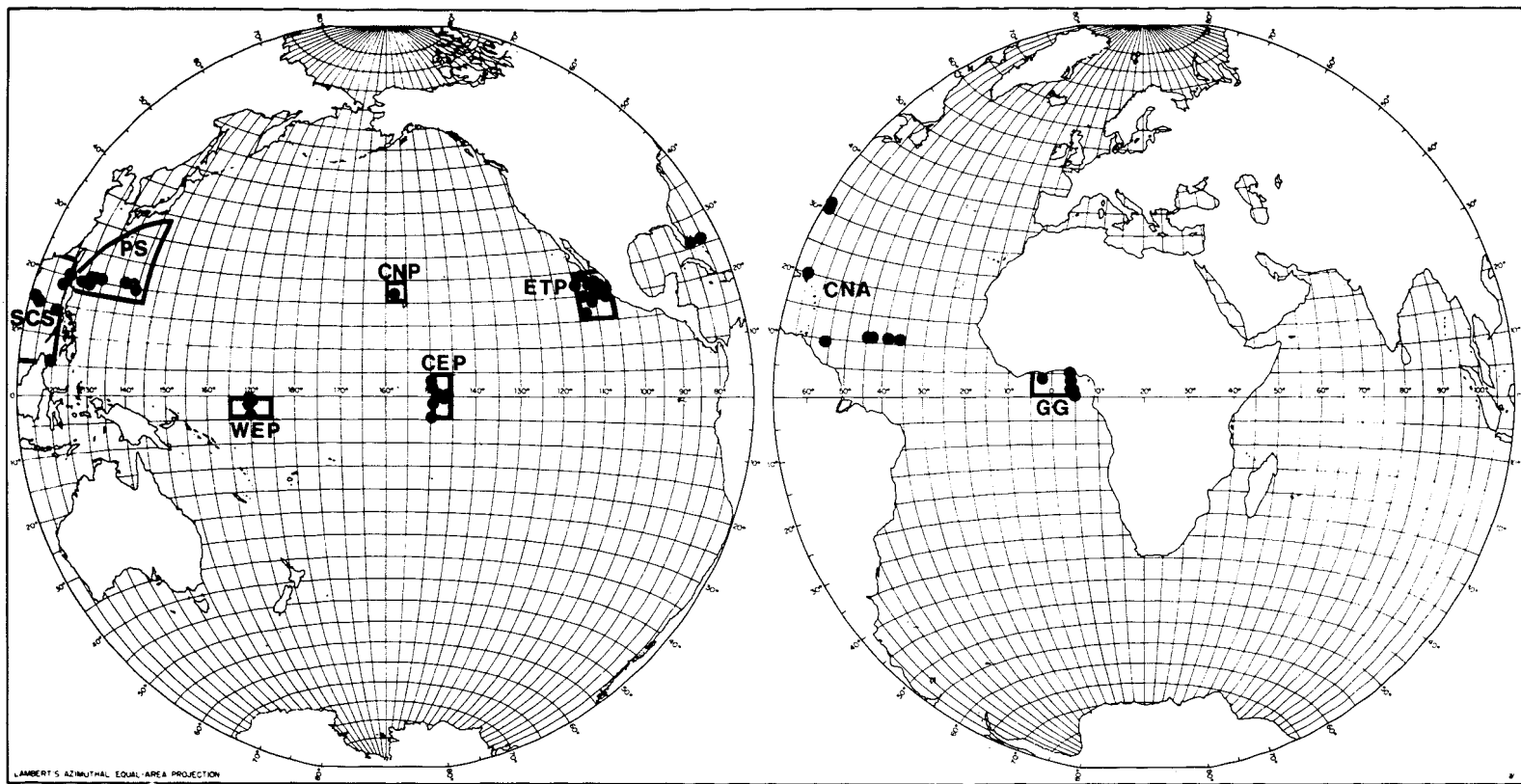


FIGURE 1.—Study areas: ETP = eastern tropical Pacific; CEP = central equatorial Pacific; CNP = central North Pacific; WEP = western equatorial Pacific; PS = Philippine Sea; SCS = South China Sea; GG = Gulf of Guinea; CNA = central North Atlantic. Localities for *Diplophos taenia* indicated by closed circles. Localities for other species were within boundaries of study areas as indicated except that all specimens of *Vinciguerria nimbaria* from the central North Atlantic were from the Ocean Acre area near lat. 32° to 33°N, long. 64°W.

TABLE 1.—Computation of rank-sum index of productivity. This table was produced by reproducing the contours or values presented by each of the authors cited in the text for each of the three measures of productivity—net primary production (NET), zooplankton concentration (ZOO), and phosphate phosphorus concentration (PO₄-P)—within the geographic limits of each of the eight areas and then ranking the eight areas with respect to one another for each measure.

Area	NET rank	ZOO rank	PO ₄ -P rank	Sum of ranks	Rank-sum
ETP	1	1	1	3	1
GG	2.5	3.5	2	8	2
SCS	2.5	3.5	4.5	10.5	3
CEP	4	5	3	12	4
WEP	7	2	4.5	13.5	5
PS	5	6	7.5	18.5	6
CNA	6	7	6	19	7
CNP	8	8	7.5	23.5	8

$W_{3,8} = 0.85, P < 0.01$

¹Data from Brinton (pers. commun.)

tropical Pacific, 2) Gulf of Guinea, 3) South China Sea, 4) central equatorial Pacific, 5) western equatorial Pacific, 6) Philippine Sea, 7) central North Atlantic, and 8) central North Pacific. In establishing the relationship between meristic counts and productivity we have compared central values of meristic counts with this rank-index value for productivity.

RESULTS

Diplophos taenia Günther

Diplophos taenia, a circumtropical mesopelagic gonostomatid, is the only species included in this study to occur in all eight study areas. Results for counts of anal fin rays, LLP photophores, and IPVALA photophores are illustrated in Figure 2. In nearly all cases counts are highest in areas of lowest productivity, lowest in areas of highest productivity, and intermediate in areas of intermediate productivity. Agreement between mean values for photophore row segments in terms of rank order by area, e.g. all four segments in the IC row, is highly significant ($W_{4,8} = 0.81, P < 0.01$, Table 2), as is the agreement between mean values for anal fin rays, LLP photophores, and IPVALA photophores ($W_{3,8} = 0.94, P < 0.01$, Table 3). This concordance allows computation of a rank-sum index for mean values of meristic counts (Table 3).

There exists no significant correlation between the observed meristic variation and temperature over the six Pacific areas ($\tau_{6} = 0.13, P > 0.20$, Table 4). Temperature data was taken from a chart of temperature at 100 m in the Pacific Ocean

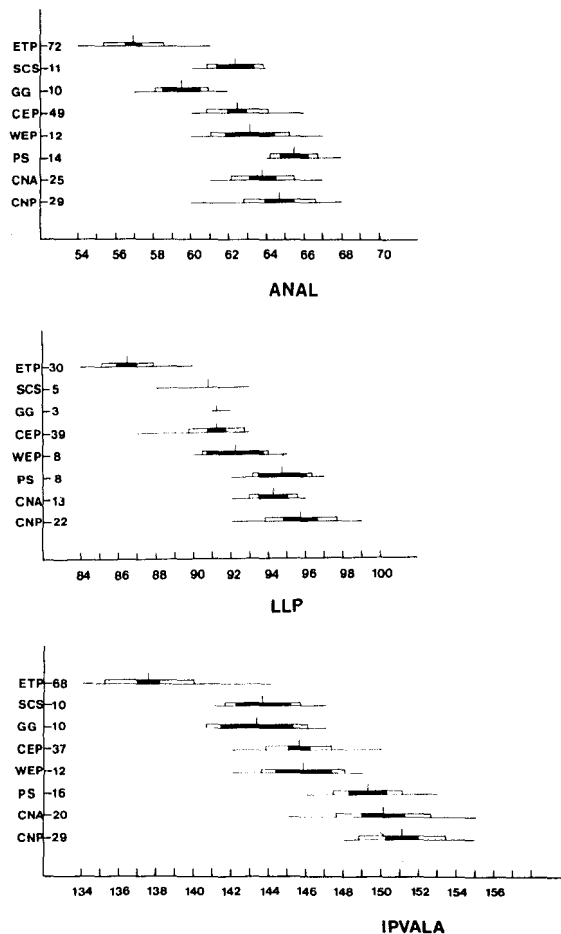


FIGURE 2.—*Diplophos taenia*. Comparison of mean (vertical line), 95% confidence limits for the mean (closed bar), one standard deviation on either side of the mean (open bar plus closed bar), and range (horizontal line) for anal fin rays (top), LLP photophores (middle), and IPVALA photophores (bottom) for specimens from eight study areas (Figure 1). Numbers on ordinate are number of specimens examined.

TABLE 2.—Agreement between segments of IC row of photophores in *Diplophos taenia*. Values are given as mean/rank. Number of specimens (*n*) is given for counts of IP and represent the minimum number of specimens counted for each character for each area.

Area	<i>n</i>	IP	PV	VAV	AC	Sum of ranks
ETP	74	15.7)8	24.9)8	15.1)8	42.0)8	32
GG	10	16.6)6	27.1)2.5	15.9)5	42.9)7	20.5
SCS	10	16.4)7	25.6)7	16.0)4	44.7)6	24
CEP	50	16.9)5	26.2)6	15.8)6	45.18)4	21
WEP	12	17.0)4	26.4)5	15.7)7	45.17)5	21
PS	18	17.1)3	26.9)4	16.3)2	46.67)3	12
CNA	25	17.4)1	27.5)1	16.2)3	46.72)2	7
CNP	29	17.3)2	27.1)2.5	16.6)1	47.5)1	6.5

$W_{4,8} = 0.812, P < 0.01$

TABLE 3.—*Diplophos taenia*, computation of rank-sum index of meristic counts and comparison with rank-sum index of productivity (from Table 1). Values are given as mean (number of specimens).

Area	Anal fin		LLP		IPVALA		Sum of ranks	Rank-sum	Productivity rank-sum
	Mean	Rank	Mean	Rank	Mean	Rank			
ETP	57.0 (72)	8	86.5 (30)	8	137.5 (68)	8	24	8	1
GG	59.5 (10)	7	91.3 (5)	5	143.3 (10)	7	19	6.5	2
SCS	62.3 (11)	6	90.8 (3)	7	143.6 (10)	6	19	6.5	3
CEP	62.4 (49)	5	91.2 (39)	6	145.54 (37)	5	16	5	4
WEP	63.2 (12)	4	92.2 (8)	4	145.75 (12)	4	12	4	5
PS	65.4 (14)	1	94.8 (8)	2	149.2 (16)	3	6	2	6
CNA	63.8 (25)	3	94.2 (13)	3	150.2 (20)	2	8	3	7
CNP	64.7 (29)	2	95.7 (22)	1	151.7 (29)	1	4	1	8

$W_{3,8} = 0.942, P < 0.01$ $Tau_8 = -0.893, P < 0.01$

TABLE 4.—*Diplophos taenia*. Comparison of rank-sum index of meristic counts (from Table 3) with temperature at 100 m ranked over the six Pacific areas. Temperature data taken from Brinton (1962).

Area	Rank	
	Counts	Temperature
CNP	1	5
PS	2	3.5
WEP	3	1
CEP	4	2
SCS	5	3.5
ETP	6	6

$Tau_6 = +0.13, P > 0.20$

given by Brinton (1962). The 100-m depth was chosen arbitrarily, but the conclusion holds if surface temperatures, whether summer or winter, are chosen. Meristic counts for *D. taenia* are lowest in specimens from the eastern tropical Pacific where temperature values are also the lowest. This is exactly opposite to the result expected if temperature were involved in determining the meristic variation observed over the six areas. In fact the data show no relationship between meristic counts and temperature for these areas. Values of salinity in the open ocean are far too conservative to be involved in determining the observed variation (Hubbs 1925; Sverdrup et al. 1942; Barlow 1961; Blackburn 1967). Although the eastern tropical Pacific is well known for a marked oxygen minimum layer (Brandhorst 1959), and oxygen concentration variation may affect the development of meristic characters (Alderdice et al. 1958; Garside 1959, 1966), in all eight areas oxygen is essentially saturated in the wind-mixed

surface layer where the larvae and probably the eggs of *D. taenia* occur. The low counts (relative to other areas) of specimens of *D. taenia* from the eastern tropical Pacific run counter to what might be expected if dissolved oxygen concentrations were involved in determining the observed meristic variation.

The rank-sum indices of meristic counts and productivity are significantly and negatively correlated ($\tau_{8} = -0.893, P < 0.01$, Table 3).

Pollichthys maui (Poll)

Pollichthys maui ranges from the western North Atlantic to the Philippine Sea. We have examined specimens of this species from the Gulf of Guinea, and the Philippine and South China seas. Results for IPVALA photophore counts (Table 5) parallel the results for *Diplophos taenia*; the counts from Philippine Sea specimens are significantly higher than counts from specimens from the South China Sea and Gulf of Guinea.

TABLE 5.—*Pollichthys maui*, IPVALA photophores.

Area	68	69	70	71	72	73	74	75	76	77	78	n	Mean \pm 95% limits
GG	1	7	5	6	1	4	—	—	—	—	—	24	70.46 \pm 0.635
SCS	—	—	1	7	2	1	—	—	—	—	—	11	71.27 \pm 0.528
PS	—	—	—	—	—	1	1	3	2	1	2	10	75.70 \pm 1.170

Vinciguerria lucetia Garman

Vinciguerria lucetia is endemic to the eastern Pacific (Ahlstrom and Counts 1958; Craddock and Mead 1970; Gorbunova 1972). The work of Ahlstrom and Counts (1958) has made the early life history of *V. lucetia* the best known of any of the species included in this report. We have not examined any specimens of *V. lucetia* in connection with this work, but the following results of the study of this species by Ahlstrom and Counts (1958) seem to be particularly relevant to this paper: 1) In *V. lucetia* the total number of myotomes is formed in late-stage eggs, prior to hatching. 2) Metamorphosis in *V. lucetia* is marked by a period of rapid change in body proportions without a marked change in standard length. The completion of metamorphosis is signaled by the complete development of all photophores, including the late-forming photophores of the posterior VAV and mid-AC segments. 3) Metamorphosis occurs at a smaller size south of lat. 25°N than north of lat. 27.5°N, with meta-

morphosis at an intermediate size in specimens from lat. 25° to 27.5°N. Mean values of vertebral and IPVALA counts are lowest in specimens taken from areas where metamorphosis occurs at a smaller size. A delay in vertebral ossification is found in specimens from areas where metamorphosis occurs at a larger size. 4) Ahlstrom and Counts (1958) report a north to south cline in mean values for IPVALA photophore counts and relate this to temperature. An east to west cline is also suggested by their data (Figure 3), with mean IPVALA counts lowest near the American continent and increasing with distance offshore. Values for productivity measures in the eastern tropical Pacific tend to fall off with increasing distance from land (Reid 1962; Koblentz-Mishke et al. 1970). If variation in photophore numbers in *V. lucetia* is related to variation in productivity, we would expect mean IPVALA counts at a given latitude to be lower near the continent and higher with increasing distance from land. Data from Ahlstrom and Counts (1958) confirm this expectation (Figure 3) for all but two latitudinal transects. Along these two transects, one just to the north of the equator, the second centered at about lat. 12°N, mean values obtained for IPVALA counts do not change or actually decrease to the

westward, an apparent contradiction of our hypothesis. However, these two zonal transects fall along zonal areas of high or elevated productivity far to the westward of the American continent, and this is true for net primary production, zooplankton standing stocks, or, as illustrated (Figure 3), phosphate-phosphorus concentration. Williams (1972) relates these zonal belts of elevated productivity to the divergence systems at the equator and at the North Equatorial Counter-current-North Equatorial Current boundary. Williams (1972) states that the zonal band at lat. 10° to 12°N is best shown by data for zooplankton stocks, but we note that this band is quite apparent for phosphate-phosphorus concentration (Reid 1962). Thus the apparently discrepant values of mean IPVALA counts from specimens of *V. lucetia* taken along these two zonal transects in fact tend to further corroborate the hypothesized inverse relationship between meristic counts and productivity.

Vinciguerria nimbaria (Jordan and Williams)

Vinciguerria nimbaria is nearly circumtropical in distribution but does not occur in the Medi-

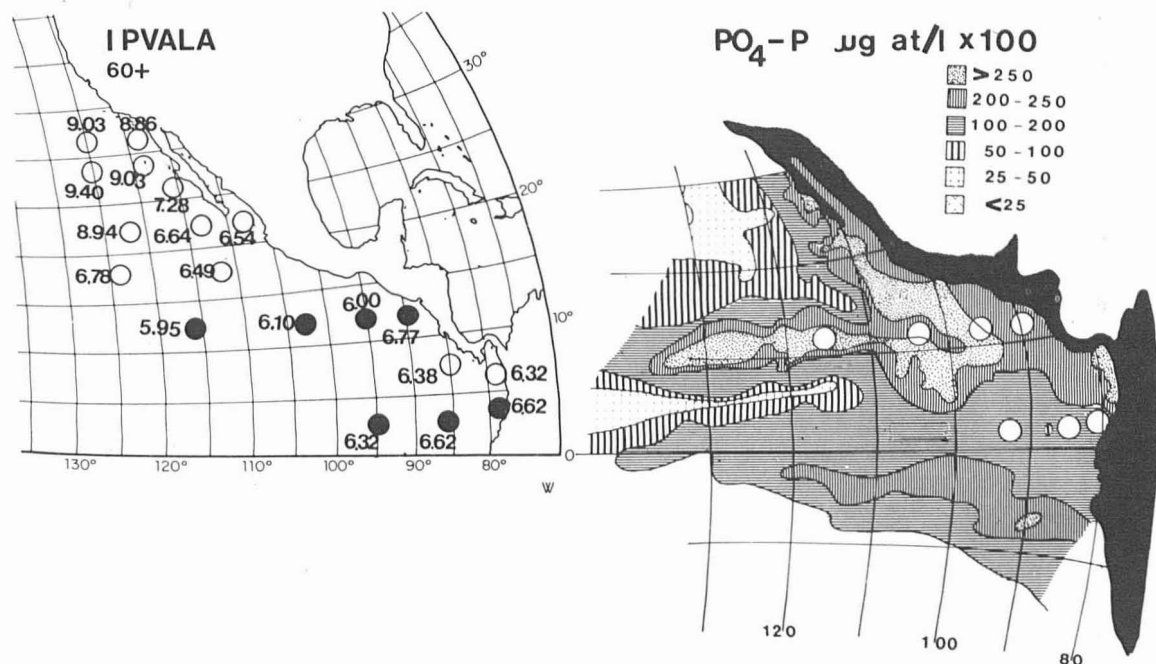


FIGURE 3.—*Vinciguerria lucetia*. Left: IPVALA photophores; values given are means based on five or more specimens taken at each locality (see text for additional explanation, data from Ahlstrom and Counts 1958). Right: phosphate phosphorus data simplified from Reid (1962).

terranean Sea nor in the eastern tropical Pacific (Ahlstrom and Counts 1958; Craddock and Mead 1970; Gorbunova 1972). The development of larvae of *V. nimbaria* is apparently quite similar to the development of larvae of *V. lucetia* (Ahlstrom and Counts 1958; Silas and George 1971). We have examined specimens of *V. nimbaria* from all of our study areas except the eastern tropical Pacific (where *V. nimbaria* is replaced by *V. lucetia*) and the western equatorial Pacific (no material available).

Counts of IPVALA photophores for specimens of *V. nimbaria* are given in Table 6. Mean values for specimens from the South China Sea, central equatorial Pacific, Philippine Sea, central North Atlantic, and central North Pacific agree in perfect rank-order with the rank-sum index of meristic counts for specimens of *Diplophos taenia* from these five areas (Table 3). The mean value of counts of IPVALA photophores of Gulf of Guinea specimens does not fit this trend, it is too high. All of our material of *V. nimbaria* from the Gulf of Guinea came from a single collection at the University of Miami (UMML 21902, lat. 0°54' to 1°05'N, long. 4°53' to 4°51'E, 23-24 May 1965). We have neither additional material of nor information on *V. nimbaria* from the Gulf of Guinea, and, for the present, we are unable to explain these anomalous results.

The values obtained for specimens of *V. nimbaria* from other study areas support our hypothesis of an inverse relationship between meristic counts and productivity. This is true for both IPVALA photophore (Table 6) and vertebral (Table 7) counts.

Counts for Arabian Sea (AS, Table 6) specimens of *V. nimbaria* are taken from Silas and George (1971). They studied specimens taken off the Malabar Coast of India and found larvae of *V. nimbaria* to be most abundant along the edge of the continental shelf from Mangalore to south of Cochin. Cushing (1971) discusses the strong upwelling system occurring along this coast during the period of the Northeast Monsoon, and notes

TABLE 7.—*Vinciguerria nimbaria*, vertebrae.

Area	39	40	41	42	n	Mean ± 95% limits
SCS	6	5	—	—	11	39.45 ± 0.351
CEP	1	23	7	—	31	40.19 ± 0.175
PS	—	3	12	8	23	41.22 ± 0.290
CNP	—	—	6	21	27	41.78 ± 0.168

that high values of productivity occur in this area over at least half of the year and are associated with the upwelling system. Silas and George (1971) found *V. nimbaria* larvae to be most abundant during the upwelling season. Values for productivity measures in this area given by Cushing (1971) approach values for the eastern tropical Pacific, are certainly larger than values for the Philippine Sea, central North Atlantic, and central North Pacific, and probably significantly larger than values for the central equatorial Pacific and South China Sea. We therefore expected values for meristic counts of specimens of *V. nimbaria* from off the Mangalore Coast to be the lowest of any of these six areas. They are (Table 6).

Chauliodus sloani Bloch and Schneider

Chauliodus sloani occurs in tropical and temperate waters from the North Atlantic to the eastern Pacific, although throughout large oceanic areas it is replaced by other species of *Chauliodus*. The remaining six species of *Chauliodus*, including the recently described *C. vasnetzovi* Novikova, are limited to smaller areas, each entirely within one ocean basin (Morrow 1961; Gibbs and Hurwitz 1967; Novikova 1972).

We have examined specimens of *C. sloani* only from our Philippine Sea and central North Pacific study areas, but data from other sources (Ege 1948; Blache 1964; Gibbs and Hurwitz 1967) have made it possible to compare our results for *C. sloani* with counts for this species from other areas, and with counts for the closely related species *C. pammelas* Alcock and *C. schmidti* Ege (Table 8). IC photophore counts of *C. sloani* from central gyral areas (CNP, CNA, PS) are higher than counts from specimens taken in the South

TABLE 6.—*Vinciguerria nimbaria*. IPVALA photophore counts. AS = study area of Silas and George (1971) along Malabar Coast of India in the Arabian Sea, data taken from their study. Counts presented as the average between right and left sizes of each specimen.

Area	64	64.5	65	65.5	66	66.5	67	67.5	68	68.5	69	69.5	70	70.5	71	71.5	72	72.5	73	n	Mean ± 95% limits
AS	2	1	1	1	2	—	1	—	1	—	—	—	—	—	—	—	—	—	—	9	65.56 ± 1.023
GG	—	—	—	—	—	—	—	—	—	—	2	2	5	2	7	1	1	—	—	20	70.43 ± 0.380
SCS	—	—	2	1	10	4	2	1	4	—	—	—	—	—	—	—	—	—	—	24	66.46 ± 0.378
CEP	—	—	—	—	2	2	1	2	14	6	4	1	—	—	—	—	—	—	—	32	67.98 ± 0.302
PS	—	—	—	—	1	2	1	4	24	26	20	37	83	36	16	4	2	1	—	257	69.60 ± 0.126
CNA	—	—	—	—	—	—	1	—	1	2	1	4	2	1	—	—	—	—	—	12	69.12 ± 0.623
CNP	—	—	—	—	—	—	—	—	—	—	—	3	18	15	5	1	1	—	—	43	70.34 ± 0.157

TABLE 8.—IC photophore variation in three species of *Chauliodus*. (NIO, northern Indian Ocean, TAA, TAB, areas of eastern tropical Atlantic discussed in text).

Species	Area	58	59	60	61	62	63	64	65	66	67	68	69	n	Mean \pm 95% limits
<i>C. pammelas</i> ¹	NIO	1	4	12	4	—	—	—	—	—	—	—	—	21	59.90 \pm 0.350
<i>C. schmidti</i> ²	TAA	—	—	1	7	32	14	—	—	—	—	—	—	54	62.09 \pm 0.186
<i>C. schmidti</i> ²	TAB	—	—	—	3	16	14	7	5	—	—	—	—	45	62.89 \pm 0.335
<i>C. sloani</i> ³	SCS	—	—	—	—	1	16	69	91	25	2	—	—	204	64.32 \pm 0.117
<i>C. sloani</i>	PS	—	—	—	—	—	—	—	3	2	4	4	—	13	66.69 \pm 0.714
<i>C. sloani</i> ³	CNA	—	—	—	—	—	—	—	—	3	6	3	1	13	67.15 \pm 0.543
<i>C. sloani</i>	CNP	—	—	—	—	—	—	—	2	9	7	2	—	20	66.45 \pm 0.386

¹Gibbs and Hurwitz 1967.²Blache 1964.³Ege 1948.

China Sea. This agrees with results for other species discussed in this paper.

The only character diagnostically separating *C. schmidti* from *C. sloani* is the lower number of serial photophores in *C. schmidti* (Morrow 1961; Blache 1964). Similarly Gibbs and Hurwitz (1967) concluded that the only characters separating *C. pammelas* from *C. sloani* were lower meristic counts (IC, VAV, vertebrae) in *C. pammelas* and greater development of the gill filaments in *C. pammelas*, with filaments both longer and with a greater number of lamellae per side. Gibbs and Hurwitz (1967) noted that the greater gill filament development of *C. pammelas* is correlated with a well-marked oxygen minimum layer in the northern Indian Ocean habitat of this species. Gill filament length may vary intraspecifically in some wide-ranging mid-water fish species (Johnson 1974).

Both *C. schmidti*, inhabiting the eastern tropical Atlantic, and *C. pammelas*, inhabiting the northern Indian Ocean, are limited to areas of high biological productivity (Ryther and Menzel 1965; Gibbs and Hurwitz 1967; Cushing 1971). Both are distinguished from *C. sloani* by lower counts of serial photophores (and vertebrae in *C. pammelas*), and essentially only by these lower counts. In both cases the lower counts apparently agree with our hypothesized relationship between meristic counts and productivity. The counts for *C. schmidti* are from specimens taken in two areas: TAA, along the west African coast from lat. 03°56' to 18°22'N, to the west and north of our Gulf of Guinea study area; and TAB, along the west African coast from lat. 01°20' to 17°53'S, to the south of our Gulf of Guinea study area (Ege 1948; Blache 1964). The counts for *C. pammelas* are from specimens taken between lat. 08° and 14°N, long. 58° to 66°E, in the Arabian Sea (Gibbs and Hurwitz 1967).

In view of other results presented in this paper,

particularly those for *Diplophos taenia*, we suggest that a reexamination of the status of both *C. pammelas* and *C. schmidti*, with additional study of meristic variation in *C. sloani* throughout the range of this species, are in order.

Results of the Antipodes Transect

An essentially experimental opportunity to test the hypothesized relationship between meristic counts and productivity was afforded by fishes taken by the Antipodes Expedition of the Scripps Institution of Oceanography in 1970. On this expedition 22 mid-water trawl collections were taken in the Philippine Sea and six mid-water trawl collections were taken in the South China Sea (Figure 4). Because of the 2,000 m or more sill depth separating these geographically contiguous areas, the upper water mass in both areas is the same and differences in physical parameters are minimal. Although the South China Sea is poorly known, there is little doubt that at least nearshore areas or areas over shelves of the South China Sea are substantially more productive than offshore areas in the Philippine Sea (Wyrтки, 1961; Sorokin 1973).

We predicted: 1) that values of meristic counts for species occurring in both the South China Sea and Philippine Sea would be lower in specimens from the South China Sea, and 2) that values of meristic counts for species occurring in the Philippine Sea would be lower in specimens taken near land and increase with increasing distance from shore.

In all four cases thus far examined (Figure 4) where differences exist in values of meristic counts from the two areas, the counts are significantly lower in specimens from the South China Sea. This supports our first prediction.

Vinciguerria nimbaria was the only species taken in sufficient abundance to allow a test of our

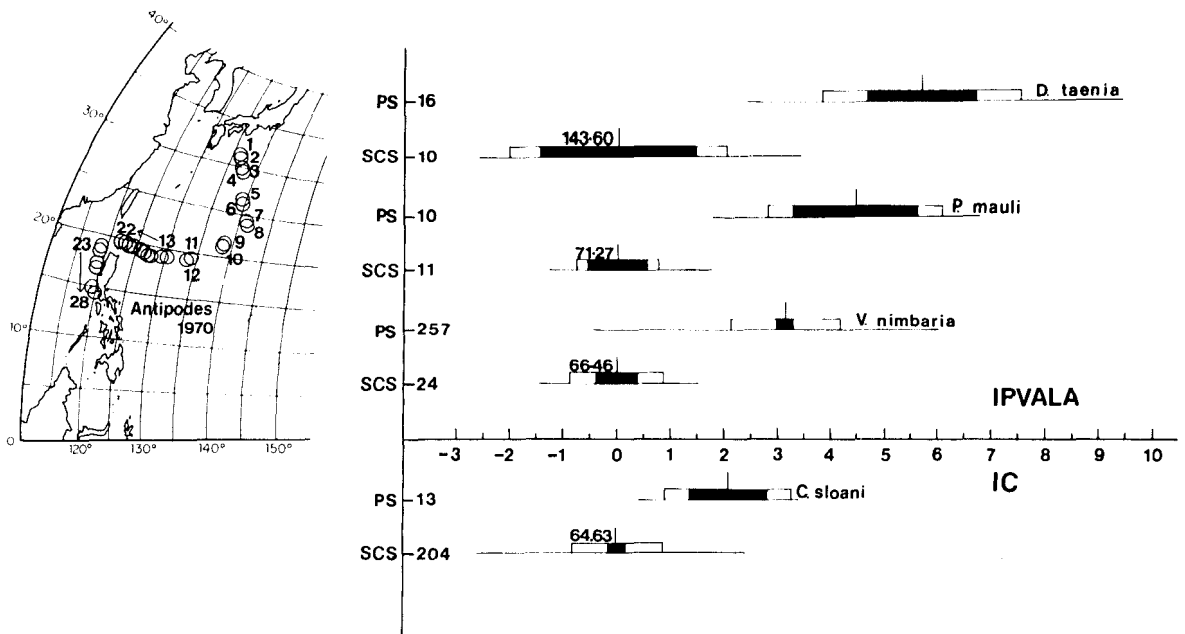


FIGURE 4.—Left: Antipodes Expedition station positions. Right: Comparison of IPVALA and IC photophore counts between specimens from South China Sea (SCS) and Philippine Sea (PS). Data presented as in Figure 2 except that mean values for South China Sea material of all four species have been set equal to zero and all other statistics are plotted as deviations from this zero point. Data for *Chauliodus sloani* from SCS are from Ege (1948); the rest is original data.

second prediction. In Table 9 mean IPVALA counts for Philippine Sea specimens of *V. nimbaria* are tested for relationship with distance of site of collection from land (Japan, Ryukyu Islands, Luzon, but not Bonin or Volcano islands). While the highest mean counts were found in specimens from the 4 stations most distant from land, the data show no relationship between mean counts and distance from land ($\tau_{11} = -0.273$, $P > 0.20$). Mean IPVALA values for specimens from each of the 11 pairs of Philippine Sea stations are significantly higher than the mean IPVALA values for specimens from the South China Sea.

DISCUSSION

One fact and two assumptions are prerequisite to our discussion of the possible explanations for the relationship between meristic counts and measures of food supply. The fact: in *Diplophos taenia*, *Vinciguerria lucetia*, and *V. nimbaria*, the values of the meristic characters we have studied are fixed at or before metamorphosis (Ahlstrom, pers. commun., Ahlstrom and Counts 1958, Silas and George 1971). This is probably also true for *Pollichthys maui* and *Chauliodus sloani*. This

means that any explanation involves factors operating on eggs and/or larvae. The assumptions: 1) that the meristic variation observed is not the result of selection for certain absolute values of the meristic counts, and 2) that the same basic mechanism underlies the variation in counts for all five species in the area studied (in this discussion we ignore results for specimens of *V. nimbaria* from the Gulf of Guinea).

There are four possibilities: 1) that the observed variation is ecophenotypic, i.e. nongenetic modification of the phenotype resulting from the effects of differing food availability conditions upon early growth and development of meristic characters; 2) that the observed variation is a by-product and indicative of genetic differences between populations in these eight areas, and that these differences reflect differing selective pressures resulting from differing conditions for early growth; 3) that the observed variation is a combination of ecophenotypy and genetic differences; and 4) that the real explanation is none of these, that a causal relationship between meristic characters and productivity does not exist, and that we have overlooked the real meaning of our results. We are unable to deal with the third pos-

TABLE 9.—IPVALA photophore counts of *Vinciguerria nimbaria* from the Philippine and South China seas. Antipodes station positions given in Figure 4. Distance from shore (Philippine Sea stations only) given in rank order from nearest to land to most distant offshore. R_m = rank of mean, R_d = rank of distance offshore.

Antipodes stations	65	65.5	66	66.5	67	67.5	68	68.5	69	69.5	70	70.5	71	71.5	72	72.5	n	Mean \pm 95% limits	R_m	R_d
1, 2	—	—	—	—	—	—	2	—	1	1	3	1	1	—	1	—	10	69.80 \pm 0.895	4	4
3, 4	—	—	—	—	—	—	3	4	3	2	4	3	3	—	—	—	22	69.47 \pm 0.456	8	5
5, 6	—	—	—	—	—	—	2	2	2	1	12	8	1	—	—	—	28	69.84 \pm 0.308	3	8
7, 8	—	—	—	—	—	—	1	—	2	4	10	3	1	—	—	1	22	69.95 \pm 0.374	2	11
9, 10	—	—	—	—	—	—	—	—	—	2	3	2	3	—	—	—	10	70.30 \pm 0.420	1	10
11, 12	—	—	—	—	—	—	1	1	2	—	1	1	—	—	—	—	6	69.17 \pm 0.930	10	9
13, 14	—	—	—	—	—	1	1	1	2	3	4	1	—	—	—	—	13	69.31 \pm 0.531	9	7
15, 16	—	—	—	—	—	—	1	—	1	—	1	2	1	—	—	—	6	69.83 \pm 1.124	5	6
17, 18	—	—	—	—	1	1	5	6	2	1	6	3	1	—	—	—	26	69.06 \pm 0.440	11	3
19, 20	—	—	—	—	—	—	1	4	—	3	3	1	1	1	—	—	14	69.54 \pm 0.604	7	2
21, 22	—	—	1	2	—	2	7	8	5	20	36	11	4	3	1	—	100	69.59 \pm 0.209	6	1
Philippine Sea, mean = 69.60 \pm 0.126																		Tau ₁₁ = -0.273 P > 0.20		
23, 24	1	1	5	1	—	1	—	—	—	—	—	—	—	—	—	—	9	66.06 \pm 0.524		
25, 26	1	—	1	1	—	—	3	—	—	—	—	—	—	—	—	—	6	66.92 \pm 1.345		
27, 28	—	—	4	2	2	—	1	—	—	—	—	—	—	—	—	—	9	66.56 \pm 0.524		
South China Sea, mean = 66.46 \pm 0.378																				

sibility and ignore the fourth possibility in our subsequent discussion.

We believe that the observed meristic variation is the result of genetic differences between populations and not the result of an ecophenotypic effect of food availability conditions on development of meristic characters. We present evidence available to support this belief, but we note that this evidence is not conclusive.

A statement of the ecophenotypic explanation is easily made. The meristic variation observed could result if the effect of low food densities upon the development of meristic characters parallels the effect of low temperature, retarding growth rates more than differentiation rates, and lengthening the period of determination of meristic characters. Because the effect of low food availability upon egg maturation appears to be a reduction of egg number and not egg size (Anokhina 1960; Blaxter 1969), any ecophenotypic effect of low food density upon meristic characters would have to operate between the onset of feeding and metamorphosis. Riley (1966) and Blaxter (1969), among others, have found for the species they have studied that the time to reach metamorphosis may be significantly increased by decreasing the density of food. Therefore an indispensable condition of the ecophenotypic explanation is that for the species studied, the final values of meristic counts are determined after the onset of feeding. If so, the meristic variation observed might result from a concordant increase in the length of the period of determination of meristic characters with a delay in time to reach metamorphosis in larvae from areas of lower productivity.

Three facts resulting from the study of the development of the eggs and larvae of *Vinciguerria lucetia* by Ahlstrom and Counts (1958) appear to support the ecophenotypic explanation: 1) Ahlstrom and Counts did find a direct relationship between size at metamorphosis (no developmental time scale is available for any of the species studied) and numbers of longitudinal photophores and vertebrae; 2) vertebral ossification and photophore formation in *V. lucetia* occur in larvae 11 mm SL or more in size, well after yolk-sac absorption and presumably after the onset of feeding; and 3) the distances between samples of *V. lucetia* utilized in construction of Figure 3 are small, much less in most cases than the distances between the eight study areas for the other species discussed in this paper. Yet the results for *V. lucetia* along the east to west transect lines apparently agree with results for the other mid-water species. We find it difficult to believe that the results for *V. lucetia* are explainable in terms of genetically distinct populations distributed along these inshore to offshore transects.

Three lines of evidence appear to contradict the ecophenotypic explanation in favor of the explanation hypothesizing that the observed meristic variation is the result of genetic differences between populations. (1) in *Vinciguerria lucetia* the total number of myomeres are formed in late stage eggs (Ahlstrom and Counts 1958). Since the number of myomeres, vertebral counts, and longitudinal photophore row counts are usually highly intercorrelated, the ecophenotypic explanation appears to be invalid in

this case. (2) The data for *Vinciguerria nimbaria* may indicate the existence of separable populations in our different study areas. This is suggested by the results for the Antipodes transect (Table 9) in which is found no clear evidence for an onshore to offshore trend toward higher IPVALA counts, despite the fact that the productivity measures are higher inshore and decrease (rapidly) to seaward (Reid 1962; Koblentz-Mishke et al. 1970). Mean values of IPVALA photophore counts for specimens from each of the 11 pairs of Philippine Sea stations are significantly higher than the mean value for South China Sea specimens. This may suggest that genetically distinct, separable populations of *V. nimbaria* are found in each area. Gill raker counts for *V. nimbaria* (Table 10) apparently support this suggestion in that counts of gill rakers are discordant with counts of IPVALA photophores (Table 6) and vertebrae (Table 7). For the four Pacific areas the counts of vertebrae and IPVALA photophores for *V. nimbaria* agree in perfect rank-order with the IPVALA photophore counts for *D. taenia* (Table 10). That this is not true for gill raker counts may indicate the existence of separable populations of *V. nimbaria* in the South China Sea, central equatorial Pacific, and the North Pacific central gyral areas (Philippine Sea, central North Pacific). (3) The ecophenotypic explanation implies that in areas of low productivity elevated meristic counts result from retardation of growth and that this retardation is the result of the average survivor being underfed compared to larvae in areas of higher productivity. As year class strength in pelagic fish populations is probably largely determined in early stages of larval life and not by the total number of eggs produced or mortality during

advanced prerecruit stages (Hempel 1965), it seems likely that selection would strongly favor any mechanisms that tended to protect the larvae of mid-water fishes occurring in areas of low productivity against starvation. The possible materials on which this selection might operate and the possible consequences on meristic characters form the basis for a second explanation of the observed meristic variation, that it is the by-product of genetic differences between separable populations in areas of low and high productivity.

Hempel (1965), Blaxter (1965), and others, concerned mainly with pelagic clupeoid fishes, have developed strong evidence that under normal circumstances the main restriction on the success of a year class occurs within a short period of larval life, the critical period of Hjort (1914, 1926) and others (e.g. Marr 1956; Schumann 1965). Selection has apparently resulted in adaptive mechanisms tending to balance the two main dangers to larval survival: the danger of starvation and the danger of predation (Blaxter and Hempel 1963; Hempel 1965).

Blaxter (1965), Hunter (1972), and others, have shown that at the onset of feeding, just before or at the time of yolk-sac absorption, surprisingly small differences in size can significantly affect the probability of larval survival. Hunter (1972) has shown for northern anchovy *Engraulis mordax* Girard, larvae that slight increments in size are associated with highly increased searching abilities, highly increased success of attempted feeding acts, and vastly diminished minimum prey density requirements for survival. Blaxter (1965) discusses the significance of the greater spectrum of particle sizes available to larger larvae in terms of increased diversity of available prey organisms. Similar findings have been reported for other fish larvae (e.g. Arthur 1956; Einsele 1965). Size at hatching, at least for Atlantic herring, *Clupea harengus* Linnaeus, is a direct function of egg size; larger larvae hatch from larger eggs. Fecundity is inversely proportional to average egg size (Baxter 1959; Blaxter and Hempel 1963; Blaxter 1969).

We believe that the meristic variation between populations occurring in areas differing in productivity values is the result of adaptations involving the adjustment of egg and larval size to the productivity regime. We believe that these adaptations reflect differences between areas of low and high productivity in the relative impor-

TABLE 10.—*Vinciguerria nimbaria*, comparison of gill raker counts with vertebral and longitudinal photophore row counts.

V. nimbaria, total gill rakers on first gill arch.												
Area	17	18	19	20	21	22	23	24	25	26	n	Mean ± 95% limits
GG	—	—	—	—	—	—	3	6	10	1	20	24.45 ± 0.386
SCS	4	7	3	1	—	—	—	—	—	—	15	18.07 ± 0.489
CEP	—	—	—	4	13	13	1	—	—	—	31	21.35 ± 0.277
PS	—	2	26	54	31	2	—	—	—	—	115	20.04 ± 0.147
CNA	—	4	8	—	—	—	—	—	—	—	12	18.67 ± 0.313
CNP	—	—	3	6	3	—	—	—	—	—	12	20.00 ± 0.469

V. nimbaria and *Diplophos taenia*, comparison of counts, given as mean (rank).

Area	<i>Vinciguerria nimbaria</i>			<i>Diplophos taenia</i>	
	Gill rakers	IPVALA	Vertebrae	IPVALA	
SCS	18.1 (1)	66.5 (1)	39.4 (1)	143.6 (1)	
CEP	21.4 (4)	68.0 (2)	40.2 (2)	145.5 (2)	
PS	20.0 (2.5)	69.6 (3)	41.2 (3)	149.2 (3)	
CNP	20.0 (2.5)	70.3 (4)	41.8 (4)	151.7 (4)	

tance of two principal dangers to larval survival: starvation versus predation.

We hypothesize that selection on mid-water fish populations inhabiting areas of low productivity has favored mechanisms tending to offset the danger of larval starvation, and that these populations will exhibit: 1) larger average egg size, 2) lower fecundity, and 3) larger average larval size at hatching and at comparable stages of development than populations living in areas of higher productivity. Advantages that might accrue to larger larvae in areas of lower productivity include increased mobility, a wider possible search volume, increased diversity of potential prey organisms, and a longer period of survivorship solely on yolk reserves.

The danger of starvation is presumably lower in areas of higher productivity but the danger of predation, resulting from presumed higher densities of potential predators on fish larvae, may be greater. Here selection may have favored increased fecundity tending to offset the danger of increased predation on larvae. We believe that in areas of higher productivity populations of mid-water fishes will exhibit: 1) smaller average egg size, 2) increased fecundity, and 3) smaller average larval size at hatching and at comparable stages of development than populations living in areas of lower productivity.

In developing this hypothesis we have largely followed Hempel's (1965) explanation for variations in egg size and fecundity between populations of herring in the eastern North Atlantic and North Sea. We note that there exists no evidence for increased predation pressure on larval populations of mid-water fishes in areas of higher productivity. It is possible to retain the main features of our hypothesis without including predation pressure by relating variation in fecundity and egg size solely to food density requirements. By definition, selection will favor maximizing reproductive output, thereby favoring fewer larger larvae in areas of low productivity where the danger of larval starvation is greater, and favoring higher fecundity (with the concomitant of smaller eggs and larvae) in areas where the danger of starvation is lessened.

There exists limited available evidence to support these predictions. Ahlstrom and Counts (1958) showed that egg size and size at hatching in *Vinciguerrria lucetia* are directly related, the smallest larvae (at a defined stage of development) are found in areas where average egg diameters are

least. They also showed that mean values of vertebral and IPVALA photophore counts are lowest in those areas where egg and larval size is least and where metamorphosis occurs earliest (i.e. at smallest size). Although no small larvae were available for this study, we were able to compare development in prejuvenile specimens of *V. nimbaria* from the central North Pacific with specimens from the central equatorial Pacific. In *V. nimbaria* the last four VAL photophores are late-forming, are laid down serially from anterior to posterior, usually the left member of a pair of VAL photophores develops just before the right, and the number yet to develop can be determined uniquely from the one to one correspondence with the posterior photophores in the VAV segment. In Figure 5 standard lengths of all available prejuvenile specimens of *V. nimbaria* from the central North Pacific and central equatorial Pacific are plotted against the number of VAL photophores left to appear. If this character can be used as an index to comparable stages of development, then at comparable stages of development the larvae from the area of lower productivity are the larger, as predicted.

We believe that the correlation between meristics and productivity results from a correlation between meristics and egg size, and that egg size and, hence, size at hatching are genetically determined features reflecting adaptation to productivity conditions. A number of authors have stated or suggested that such a correlation exists (Ahlstrom and Counts 1958; Lindsey 1958, 1961; Garside

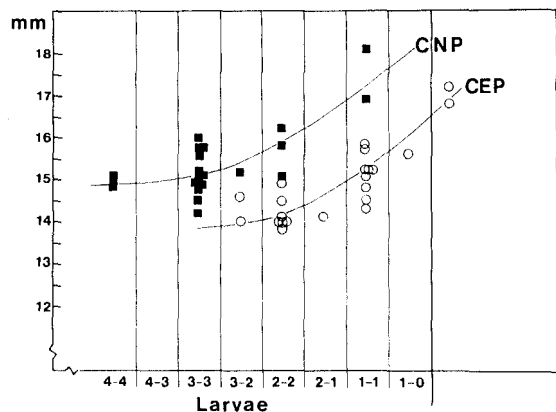


FIGURE 5.—Size of larvae of *Vinciguerrria nimbaria* from the central North Pacific (CNP) and the central equatorial Pacific (CEP) at comparable stages of development. Ordinate: standard length in millimeters. Abscissa: number of VAL photophores yet to form (determined from VAV count) on each side of each specimen. Lines fitted by eye.

and Fry 1959). Lindsey and Ali (1971) have recently argued against this suggested relationship, despite the fact that their data showed a direct relationship between the number of anal fin rays and egg size in the medaka, *Oryzias latipes*. Blaxter and Hempel (1963) found no relationship between incubation time and egg size in herring, but did find a positive correlation between time to yolk sac absorption and egg size. If this correlation is true for the mid-water fishes considered in this report, if the correlation continues beyond the point of yolk sac absorption, and if the meristic characters in question are determined after hatching, it might result in a longer period of determination of these characters in larvae from larger eggs.

We lack essential developmental and ecological information to complete our hypothesis. We know little or nothing for our mid-water species about age and size at first spawning, number of spawnings per female, fecundity, seasonality of reproduction, course of larval development, or factors actually determining survivorship of larvae. The answer to the question of mechanism awaits the comparison of these population parameters between populations in areas of high and low productivity.

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MATERIAL EXAMINED

Diplophos taenia. The material examined of this species is listed in Johnson and Barnett 1972. Supplementary station list of materials examined for a study of meristic variation in *Diplophos taenia* Guenther. Ref. Ser. Scripps Inst. Oceanogr. 72-4, 1-8 (unpublished manuscript available from the Library, Scripps Institution of Oceanography, La Jolla, Calif).

Pollichthys mauii. GG: 24 (28.5-46.9), UMML 22881 (1), UMML 24132 (1), UMML 24237 (1), UMML 24266 (3), UMML 24658 (6), UMML 27884 (6), UMML 27929 (5), UMML 28159 (1). SCS: 11 (21.1-31.1); SIO 61-744 (1), SIO 69-20, (10); PS: 10 (33.8-49.9); SIO 70-308 (1), SIO 70-309 (1), SIO 70-334 (2), SIO 70-337 (2), SIO 70-340 (4).

Vinciguerria attenuata. SCS: 71 (13.0-37.8); SIO 70-341 (5), SIO 70-343 (5), SIO 70-344 (52), SIO 70-345 (5), SIO 70-346 (3), SIO 70-347 (1). PS: 71 (13.0-28.1); SIO 70-308 (12), SIO 70-309, (10), SIO 70-310 (6), SIO 70-311 (12), SIO 70-314 (11), SIO 70-318 (1), SIO 70-333 (15), SIO 70-334, (1), SIO 70-337 (2).

Vinciguerria nimbaria. GG: 20 (21.0-37.5); UMML 21902 (20). SCS: 35 (11.7-32.0); SIO 70-341 (4), SIO 70-343 (5), SIO 70-344 (10), SIO 70-345 (5), SIO 70-346 (5), SIO 70-347 (6). PS: 729 (11.6-39.9); SIO 70-306 (63), SIO 70-308 (6), SIO 70-309 (18), SIO 70-310 (23), SIO 70-311 (29), SIO 70-314 (45), SIO 70-318 (52), SIO 70-326 (7), SIO 70-327 (3), SIO 70-328 (12), SIO 70-329 (22), SIO 70-331 (2), SIO 70-332 (11), SIO 70-333 (173), SIO 70-334 (15), SIO 70-336 (6), SIO 70-337 (14), SIO 70-339 (2), SIO 70-340 (226). CEP: FMNH (Field Museum of Natural History) 77100 32 (16.9-36.0). CNA: USNM,

Ocean Acre Stations, all material from ca. lat. 32-32.5°N., long 64°W. 12(19.1-35.8); 12-17C (1), 12-18A (2), 12-18B (2), 12-28B (1), 12-34C (1), 12-35C (1), 12-62 (1), 12-80 (1), 12-81 (1), 12-86 (1). CNP: 49 (14.1-31.0); UH 69-11-5 (49).

Chauliodus sloani. PS: 14 (42.2-214.5); SIO 70-306 (3), SIO 70-311 (2), SIO 70-326 (1), SIO 70-334 (8). CNP: 20, SIO 71-301 (1), SIO 71-307 (1), SIO 71-309 (5), SIO 71-373 (1), SIO 72-11 (2), SIO 72-16 (1), SIO 72-22 (1), SIO 72-25 (2), SIO 73-142 (1), SIO 73-149 (1), SIO 73-155 (1), SIO 73-158 (2), SIO 73-159 (1).

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