

# On the Quantity and Types of Food Ingested by Peruvian Anchoveta, 1953-1982\*

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## Abstract

This contribution presents the results of a first analysis of a computerized database on the food and feeding habits of the Peruvian anchoveta (*Engraulis ringens*) for the years 1953 to 1982, besides serving as (partial) documentation for the same database, which documents, on an unaggregated basis, nearly 10,000 anchoveta stomach contents and ancillary information. Detailed phylogenetic "trees" were graphed whose "branches" represent different food items and whose frequency of occurrence is reported. The diel periodicity of mean stomach contents in over 5,000 anchoveta was used to estimate their food consumption. Feeding starts near noon and is continuous until near midnight. A ration of 0.45 g day<sup>-1</sup> (mixed phyto- and zooplankton) was estimated from anchoveta with a mean live weight of 20.4 g. This implies, given a mean total mortality of  $Z = 4.5 \text{ year}^{-1}$ , a relative population consumption rate of 3.3%/day. The fraction of zooplankton in the mixed phyto- and zooplankton diet of anchoveta was found to increase with distance from the coast, southern latitude and temperature.

## Resumen

En esta contribución se presentan los resultados de un primer análisis de la base de datos computarizada sobre el alimento y hábitos alimenticios de la anchoveta peruana (*Engraulis ringens*) para los años 1953 a 1982, los que además sirven como documentación (parcial) para la misma base de datos, cuyos documentos sobre una base desagregada, llegan casi a los 10,000 contenidos estomacales de anchoveta y adicional información. Se grafican "árboles" filogenéticos cuyas "ramas" representan los diferentes items alimentarios y cuya frecuencia de ocurrencia es reportada. La alimentación empieza cerca del medio día y se continúa hasta cerca de la medianoche. Para estimar el consumo de alimento se utilizó la periodicidad diaria del contenido estomacal promedio de más de 5,000 anchovetas. Se estimó una ración de 0.45 g·día<sup>-1</sup> (mezcla de fito- y zooplancton) para anchovetas de un peso promedio de 20.4 g. Esto significa que, dado un promedio de mortalidad de la población de  $Z = 4.5 \text{ año}^{-1}$ , la tasa de consumo de la población es de 3.3%/día. La fracción de zooplancton en una dieta mixta de fito- y zooplancton se incrementa con la distancia de la costa, con la latitud hacia el sur y con la temperatura.

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## Introduction

This contribution presents a preliminary analysis of the food types and food consumption of the Peruvian anchoveta (*Engraulis ringens*), based on the data of Rojas de Mendiola (this vol.) and Alamo (this vol.), covering the years 1953 to 1982. No attempt will be made here to extract all information contained in the now computerized Rojas/Alamo database. Rather we aim at providing a framework for future, more detailed studies on the feeding habits of anchoveta in relation to fluctuations of the Peruvian upwelling system.

This contribution consists of three parts:

- i) presentation and partial reduction of the taxonomic diversity of anchoveta food items;
- ii) testing of some extant hypotheses on the spatial and temporal variations of the zooplankton fraction (ZF), i.e., the ratio zooplankton/(zooplankton + phytoplankton) in anchoveta stomach contents; and
- iii) estimation of the daily ration of an "average" anchoveta and of the relative food consumption of the entire population.

Part (i) serves three purposes: (a) to illustrate the wide range and the frequency of occurrence of food items recorded from anchoveta stomachs, (b) to identify the taxonomic affinities of these food items and (c) to assign these food items to a small number of taxonomically homogeneous groups, such as needed for future quantitative analyses.

The hypotheses involved in Part (ii) are: (a) that anchoveta in the north of Peru have lower ZF values than those in the south, (b) that anchoveta sampled inshore should have a lower ZF than anchoveta sampled offshore (Vinogradov 1981), (c) that high sea surface temperatures (SST) are associated with higher ZF and (d) that anchoveta in the 1950s and 1960s had higher ZF than in the following decades (Palomares et al. 1987).

Finally, we shall present in Part (iii) the first rigorous attempt to estimate the daily ration of anchoveta based on stomach content data. Our aim here is to allow comparison with and a calibration of ration estimates based on metabolic considerations (Villavicencio 1981; Tsukayama and Sanchez 1981; Palomares et al. 1987), and eventually, to allow quantitative modelling of the transfer of primary production off Peru (Chávez et al., this vol.; Mendo et al., this vol.) to higher trophic levels.

For general orientation, we present a photo of an anchoveta (Fig. 1.) and, in Figs. 2, 3 and Table 1, some key anatomical features of anchoveta that are related to food capture and processing.

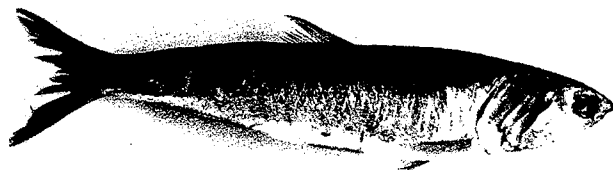


Fig. 1. Thawed, 13-cm specimen of anchoveta *Engraulis ringens* (Photo: Mark Prein).

Fig. 1. Anchoveta de 13 cm, espécimen descongelado (Foto: Mark Prein).

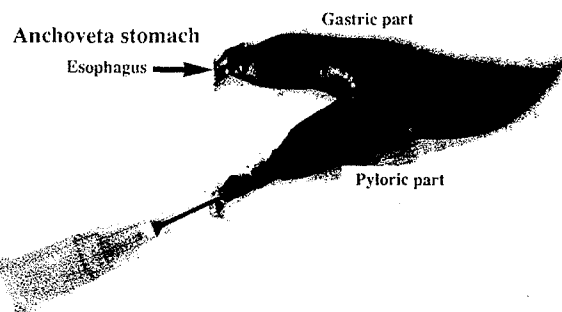


Fig. 2. Stomach of an anchoveta, slightly distended through injection of water. Note gastric and pyloric parts of the stomach (Photo: Mark Prein).

Fig. 2. Estómago de anchoveta ligeramente distendido después de inyectársele agua. Nótese la parte gástrica y pilórica del estómago. (Foto: Mark Prein).

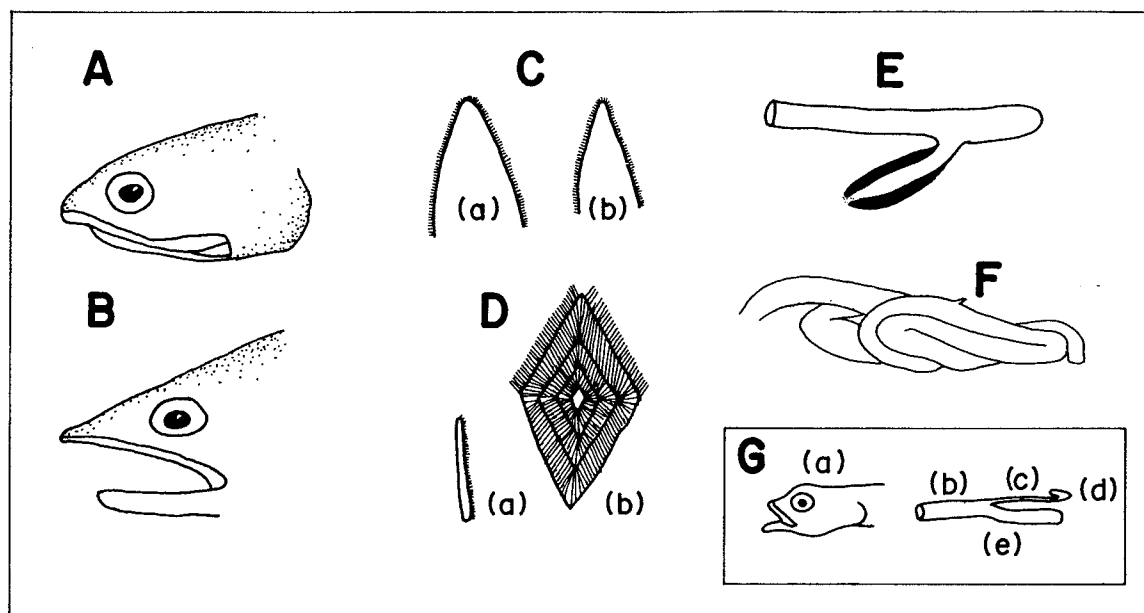


Fig. 3. Anatomical features of anchoveta related to its food and feeding habits: (A) The inferior mouth of anchoveta. (B) The same, open. (C) Villiform teeth (a) superior maxilla, (b) inferior maxilla. (D) Gill rakers (a) a single, enlarged gill raker, (b) the filtering apparatus. (E) The stomach and the thick-walled pylorus (see also Fig. 2). (F) The intestine. (G) Larval organs (a) head, (b) foregut, (c) ductus pneumaticus, (d) caudal part of gas bladder, (e) stomach. (Adapted from Vegas-Velez 1981; Harder 1957, 1960)

Fig. 3. Características anatómicas de la anchoveta relacionadas con su alimento y hábitos alimenticios: A. Boca de la anchoveta; B. la misma abierta; C. Dientes de apariencia vellosica a) maxila superior, b) maxila inferior; D. Branquispinas a) una sola branquispina ampliada, b) aparato filtrador; E. Estómago y las paredes gruesas del píloro (ver también Fig. 2); F. Intestino; G. Especimen larval a) cabeza, b) conducto alimentario, c) tubo neumático, d) parte caudal de la vejiga natatoria, e) estómago. (Adaptado de Vegas-Vélez 1981; Harder 1957, 1960).

Table 1. Selected information on the intestinal tract of anchoveta *Engraulis ringens*.<sup>a</sup>  
Tabla 1. Información seleccionada sobre el tracto digestivo de la anchoveta *Engraulis ringens*.

Item	Measurement	Mean value	Mean in % of S.L.
Standard length	from tip of snout to end of hypural bone	108	100
Height	maximum height of fish between dorsal and ventral edge of body	20.0	18.5
Width	maximum width of fish	12.5	11.6
Visceral cavity	length of visceral cavity	43.2	40.0
"Branchial gut"	from tip of snout to begin of esophagus	30.5	28.2
"Foregut"	from begin of esophagus to begin of stomach (bulge)	16.5	15.3
Stomach	from begin of stomach to pylorus	12.0	11.1
Intestine	from pylorus to anus	125	116
All digestive tract	from tip of snout to anus	184	170

<sup>a</sup>Adapted from Harder (1960), based on three specimens collected near Guañape, Peru, in 1954, by staff of the Inter-American Tropical Tuna Commission; all lengths are in mm.

## Materials and Methods

The data used for Part (i) of this contribution are the raw data sheets of Rojas de Mendiola (this vol.) and Alamo (this vol.), which include, for each anchoveta sampled, up to six of the most abundant food items. Each of these food items was listed, and the total number of occurrences was recorded (no distinction was made between the periods covered by the data of Rojas de Mendiola, this vol., and those of Alamo, this vol.). Then, the taxonomic affinities of each item were identified, using standard references (e.g., Bougis 1976; Mann 1978 or Barnes 1980) and phylogenetic "trees" were constructed which included only organisms recorded as anchoveta food item. Finally, fifteen groups of food items were defined, whose boundaries represent compromises between taxonomic homogeneity and the need for a roughly similar number of occurrences within each group.

Part (ii) is based on analysis of the ZF values in the Rojas/Alamo database. Fig. 4 presents the geographic distribution of entries in this database, as well as definitions for:

- (a) the northern, central and southern sections of the Peruvian coast (all locations north of 9°59'S, 10°00' - 13°59'S and all locations south of 14°00'S, respectively), and
- (b) the inshore, intermediate and offshore parts of the coastal strip inhabited by anchoveta.

With regard to hypotheses (c) and (d) above, the three temperature ranges selected are  $<17$ ,  $\geq 17$  to  $\leq 19.9$  and  $\geq 20^{\circ}\text{C}$ , while the three periods considered are 1953 to 1974, 1975 to 1978 and 1979 to 1985. The cutoff points used for hypotheses (a) to (d) were selected such as to allow enough entries to be represented in each of the three groups used for the comparisons, and also such as to be consistent with an earlier subdivision (that between northern, central and southern anchoveta stock and/or substock, pertaining to hypothesis (a)). All analyses involving ZF values were performed after application of an arcsine transform, which has the effect of normalizing percentage values (Sokal and Rohlf 1981; Sachs 1984), a fact which we confirmed for the data at hand. Differences in mean transformed ZF values were tested for significance using t-tests (Sachs 1984).

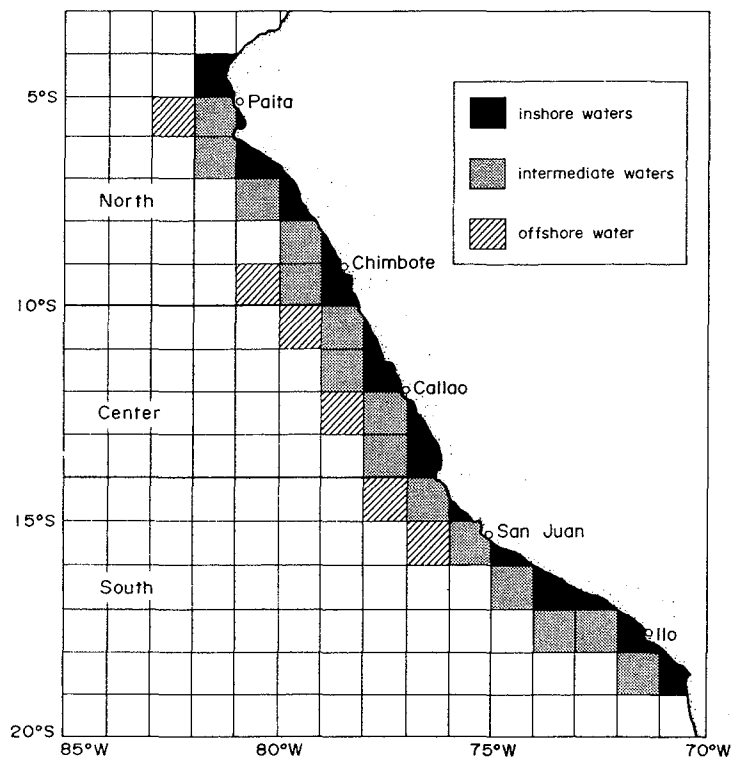


Fig. 4. Definition of the southern, central and northern zone of the Peruvian coast, and of inshore, intermediate and offshore waters as used in this contribution. All shaded squares contain anchoveta samples (see text).

*Fig. 4. Delimitación de las zonas Sur, Centro y Norte de la costa peruana; y de las aguas costeras, intermedias y afuera de la costa, como se presentan en esta contribución. De todos los cuadros sombreados se obtuvieron muestras de anchoveta (ver texto).*

Part (iii) of this contribution was performed in a number of steps best presented jointly, then discussed separately in more detail:

- (1) Establishment of a quantitative relationship between degrees of fullness and relative stomach content weight in those anchoveta for which both types of entries were available;
- (2) Estimation of relative stomach content weight using the relationship above in all anchoveta for which only the degree of fullness was available, and transformation of absolute weight of stomach content into relative weight of stomach content in all anchoveta for which both stomach content weight and body weight were available;
- (3) Computation of mean relative weight of stomach content of anchoveta caught in different parts of a 24-hour cycle; and
- (4) Application of the model of Sainsbury (1986) for estimation of daily ration from the data in (3).

The scale expressing degree of stomach fullness used by Rojas de Mendiola (this vol.) and Alamo (this vol.) has four steps: "empty", "half empty", "half full" and "full". Two of these are straightforwardly reexpressed as % values: "empty" = 0% and "full" = 100%. Rojas de Mendiola's definition of "half empty" differs from that of "half full", however, and these two categories could therefore not be set equal to each other and to 50%.

We have, therefore, used an iterative approach, i.e., identified the % value for "half empty" (and hence also the % value of "half full" = 100 - half empty) which maximized the correlation between (transformed) relative stomach weight and degree of fullness. Also, we have estimated the parameter  $b$  in the relationship:

$$\sqrt{\frac{(\text{stomach content weight}) * 100}{\text{body weight}}} = b * (\% \text{ fullness}) \quad \dots 1)$$

where the square root transformation was used to normalize the variance (the corresponding linear regression had an intercept not significantly different from zero, hence the reduced form of equation (1)).

Once the optimal % values for "half empty" and "half full" and the corresponding version of equation (1) were identified, relative stomach content weights ( $S_{(R)}$ ) were derived for all anchoveta for which only fullness values had been available and a file was created which also included  $S_{(R)}$  values computed directly from weight of stomach content/body weight data pairs.

To describe a diurnal cycle of mean stomach content weights, the available  $S_{(R)}$  values were then grouped into 16 classes of 1.5 h each, i.e., 00h01' - 01h30' (mid-point 00h45'), 01h31' - 03h00' (mid-point 02h15'), etc. These groupings appear optimal given the relatively low number of nighttime observations, and the need to use an appropriate number of classes, i.e., between 12 and 20 (Sokal and Rohlf 1981).

In view of the non-normal distribution of the  $S_{(R)}$  values within each temporal class, we abstained from using the arithmetic mean as a measure of central tendency. Rather, we used

$$\bar{X} \approx 0.33 (D_1 + \tilde{X} + D_9) \quad \dots 2)$$

where  $D_1$  and  $D_9$  are the 1st and the 9th deciles, respectively, and  $\tilde{X}$  the median, i.e., the 5th decile (Sachs 1984). The corresponding estimate of standard deviation is

$$\text{s.d.} \approx 0.39 (D_9 - D_1) \quad \dots 3)$$

Standard errors (s.e.) were computed from

$$\text{s.e.} = \text{s.d.} * \sqrt{n} \quad \dots 4)$$

The model used here for the estimation of food consumption (i.e., daily ration, or  $R_d$ ) from the diurnal dynamics of stomach contents is the simpler of two models presented by Sainsbury (1986).

The model assumes that the 24-hour diurnal cycle can be split into two phases:

- (a) a feeding phase, during which feeding occurs at a constant *rate*, while a constant *fraction* ( $c$ ) of the stomach content is (simultaneously) being evacuated, and
- (b) a nonfeeding phase, during which only stomach evacuation takes place.

If, for a 24-hour cycle

$\tau$  is the "physiological time," measured from the beginning of feeding period (in hour),

$S_\tau$  the mean weight of the stomach content at time  $\tau$ ,

$\alpha$  the feeding rate (in  $g \cdot \text{hour}^{-1}$ ),

$c$  the evacuation rate (in  $\text{hour}^{-1}$ ),

$T_m$  the duration (in hour) of the feeding period, and

$S_r$  the residual stomach content at the beginning of feeding period,

then the mean weight of stomach content can be calculated as

$$S_\tau = \frac{\alpha}{c} + \frac{(cS_r - \alpha)}{c} e^{-c\tau} \quad \dots 5a)$$

during feeding time when  $0 < \tau < T_m$ , and

$$S_\tau = \left[ \frac{\alpha}{c} + \frac{(cS_r - \alpha)}{c} e^{-cT_m} \right] e^{-c(\tau - T_m)} \quad \dots 5b)$$

during nonfeeding time when  $T_m < \tau < 24$  hours,

wherein

$$S_r = \frac{\alpha(e^{-c(24h - T_m)} - e^{-c \cdot 24h})}{c(1 - e^{-c \cdot 24h})} \quad \dots 5c)$$

The daily ration of food consumed is calculated as  $R_d = \alpha T_m$ .

Fitting of equation (5) to our data was performed after smoothing the data over three time intervals, using a BASIC program implemented on an MS-DOS computer<sup>a</sup>, and representing a modified version of a FORTRAN listing kindly supplied by Dr. K. Sainsbury (CSIRO, Hobart, Australia, pers. comm.)

Estimation of the gross food conversion efficiency of anchoveta ( $K_1 = \text{growth increment/food ingested}$ , see Ivlev 1966) was based on the equation

$$K_1 = (dw/dt)/R_d \quad \dots 6)$$

with growth increment (= growth rate) obtained from

$$dw/dt = 3KW ((W_\infty/W)^{1/3} - 1) \quad \dots 7)$$

<sup>a</sup> Available from the first author.

i.e., from the first derivative of the von Bertalanffy Growth Function (VBGF). The VBGF has, for growth in weight the form

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \quad \dots 8)$$

where  $W_t$  is the weight at age  $t$   
 $W_\infty$  the asymptotic weight  
 $K$  a growth constant, and  
 $t_0$  the "age" at weight zero.

The estimate of  $K_1$  was then used to estimate the parameter  $\beta$  in the equation:

$$K_1 = 1 - (W/W_\infty)^\beta \quad \dots 9)$$

through

$$\beta = \log_{10} (1 - K_1) / \log_{10} (W/W_\infty) \quad \dots 10)$$

Using  $\beta$  and  $K$ , food consumption ( $Q$ ) per unit biomass ( $B$ ) of an age-structured population ( $Q/B$ ) can be estimated using a simplified version of the model of Pauly (1986), of the form

$$Q/B = \frac{\int_0^\infty \frac{(dw/dt) e^{-Z(t-t_0)}}{K_1(t)} dt}{\int_0^\infty W_t e^{-Z(t-t_0)} dt} \quad \dots 11)$$

where  $K_{1(t)}$  is the gross conversion efficiency as a function of fish age (obtained by combining equations (8) and (9)),  $Z$  is the exponential rate of total mortality in the population studied, and  $W_t$  is obtained from equation (8).

Transfer efficiency ( $E_t$ ) was obtained, finally, from  $E_t = Z * (B/Q)$ , i.e., by multiplying the inverse of the relative food consumption by the production biomass ratio (because  $Z = P/B$  under steady-state conditions, see Allen 1971).

## Results and Discussion

Figs. 5 and 6 present taxonomic "trees" of anchoveta food items listed in the raw data sheets of B. Rojas de Mendiola and A. Alamo, along with number of occurrences. Figs. 7 to 9 provide details on three important "branches" of these trees, the Protozoa (with emphasis on the dinoflagellates), the Chrysophyta (i.e., the diatoms), and the crustaceans (with emphasis on the copepods). Altogether 259 different food items were identified, from nearly 10,000 individual anchoveta, and this number would have been far greater had it not been for the fact that only the 5-6 most abundant food items were recorded from each stomach examined.

An approach is presented in Table 2 to arrange these food items into 15 more or less homogeneous groups with roughly comparable numbers of occurrences (ratio of smallest to largest = 1:27, i.e., 1.43 log units). Of these 15 groups, 14 are used for the food type fields (I-V) in the computerized database of Rojas de Mendiola (this vol.) and Alamo (this vol.). (The 15th group, i.e., anchoveta eggs, is listed separately, see below.) Table 3 gives details on the "miscellaneous items" of Table 2.

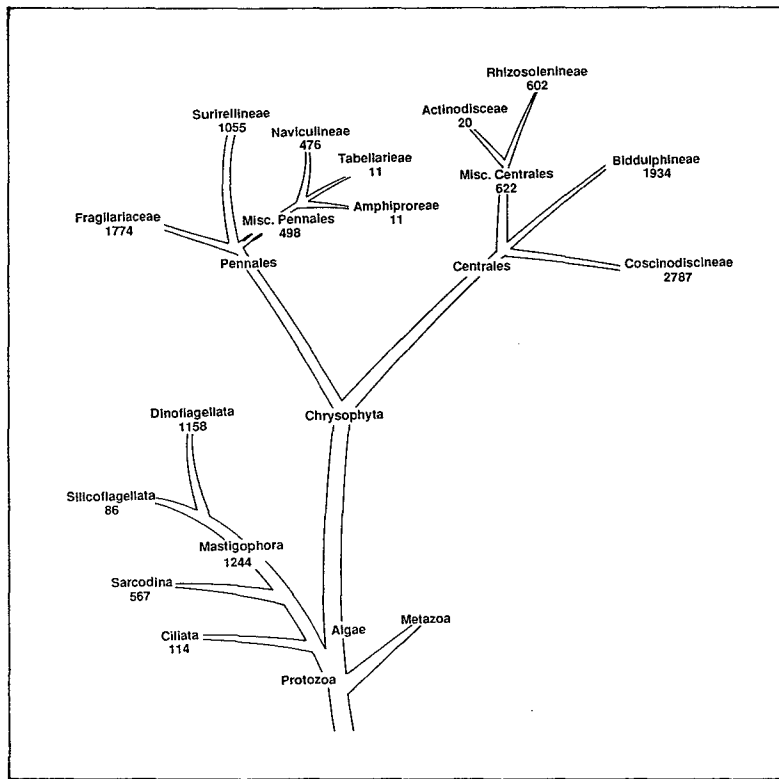


Fig. 5. Taxonomic "tree" for single cell organisms ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences; see also Fig. 6).  
 Fig. 5. Diagrama taxonómico (posición genealógica) de los organismos unicelulares ingeridos por la anchoveta, 1953 a 1982. (Los números indican la ocurrencia; ver también Fig. 6).

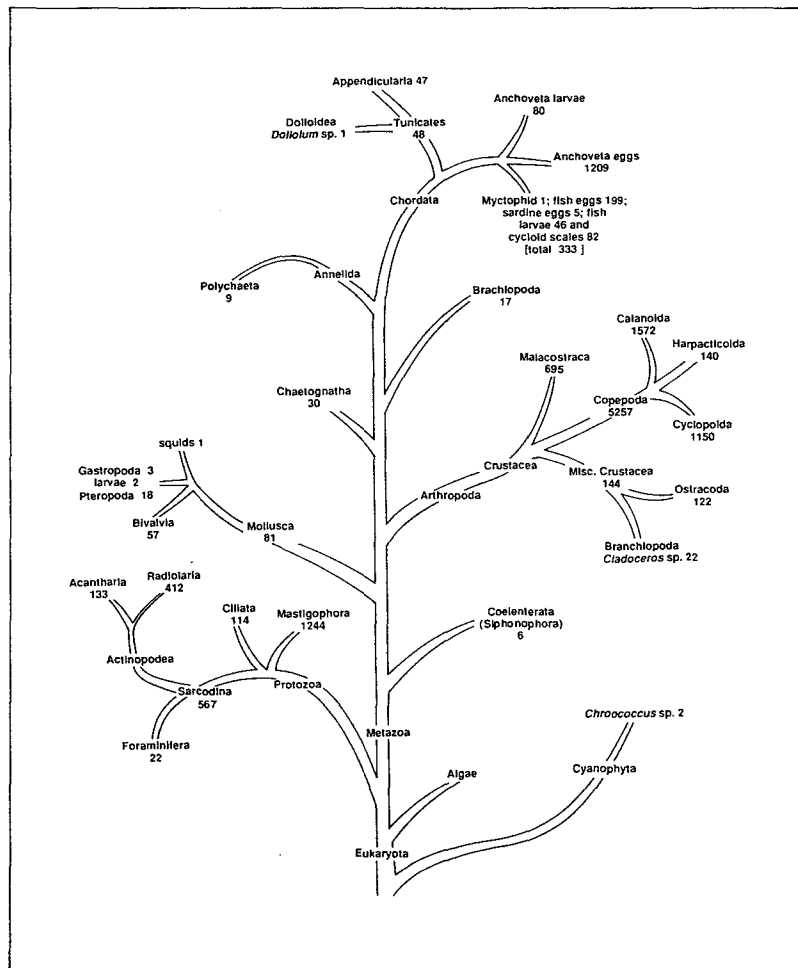


Fig. 6. Taxonomic "tree" emphasizing metazoan organisms ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences; see also Fig. 5).  
 Fig. 6. Diagrama taxonómico que resalta los metazoos ingeridos por la anchoveta, 1953 a 1982 (los números indican la ocurrencia, ver también Fig. 5).

Table 4 and Fig. 10 present the results of the tests of four different hypotheses relating to changes in the zooplankton fraction (ZF) in the diet of anchoveta.

These results suggest (a) that anchoveta in the northern/central part of Peru rely on zooplankton less than do their counterparts on the south of Peru, (b) that mean ZF significantly

Table 2. Taxonomic and other grouping used to describe the food of Peruvian anchoveta.  
*Tabla 2. Grupos taxonómicos usados para describir el alimento de la anchoveta peruana.*

Group number	Taxa included	Details in	No. of occurrences <sup>a</sup>
1	Miscellaneous items	Table 3	485
<i>Phytoplankton</i>			
2	Fragilariaceae	Fig. 8	1,643
3	Surirellineae	Fig. 8	1,044
4	Misc. Pennales	Fig. 8	473
5	Coscinodiscineae	Fig. 8	3,487
6	Biddulphiaceae	Fig. 8	1,646
7	Misc. Centrales	Fig. 8	608
8	Mastigophora	Fig. 7	621
<i>Zooplankton</i>			
9	Sarcodina + Ciliata	Fig. 7	1,069
10	Misc. invertebrates <sup>b</sup>	Fig. 6	149
11	Malacostraca	Fig. 9	688
12	Copepoda	Fig. 9	3,998
13	Misc. crustaceans <sup>c</sup>	Fig. 9	285
14	Misc. chordata <sup>d</sup>	Fig. 6	442
15	Anchoveta eggs <sup>e</sup>	Fig. 6	- e

<sup>a</sup>These numbers do not match those in Figs. 6-9 because for those, the component taxa of all groups (1-15) were counted separately, as recorded on the raw data sheets of B. Rojas de Mendiola and of A. Alamo, while for this table, only group occurrences in the computerized database were counted.

<sup>b</sup>Including Coelenterates, Chaetognaths, Polychaetes, Mollusks and Brachiopods.

<sup>c</sup>Including Ostracoda and Branchiopoda.

<sup>d</sup>Including tunicates, small fish, anchoveta and other fish larvae, fish scales and non-anchoveta fish eggs.

<sup>e</sup>Not included as food item 15 in the Rojas/Alamo database; listed separately as "no. of eggs per stomach".

Table 3. Reported occurrences in anchoveta stomachs of items not attributable to any definite taxon.<sup>a</sup>

*Tabla 3. Relación de las ocurrencias en los estómagos de anchoveta de ítems no atribuibles a un definido grupo taxonómico.*

Item	Occurrences (in %)
Invertebrate eggs	24.1
Invertebrates	1.7
mucus	3.5
Unidentified material	12.8
Organic material	0.6
Plankton	1.5
Phytoplankton <sup>b</sup>	29.5
Zooplankton	17.5
Algae	1.7
Detritus	5.0
Fibers	0.4
Chromatophores	1.7
Total number of occurrences	485

<sup>a</sup>These items are listed as "miscellaneous items" in Table 2.

<sup>b</sup>Including 2 occurrences of Cyanophyta.



Fig. 7. Protozoan taxa ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences; see also Fig. 5).

Fig. 7. Protozoos ingeridos por la anchoveta peruana, 1953 a 1982 (los números indican la ocurrencia; ver también Fig. 5).

increases with offshore distance, (c) that more zooplankton is consumed when SST is high and (d) that the mean ZF values were different in the three sampling periods considered here.

Interpretation of these results is straightforward in the case of (a), (b) and (d). In the case of hypothesis (b), we have indeed a rather stunning confirmation of the process described by Vinogradov (1981) wherein a plume of upwelled water enriches itself with zooplankton as it moves "downstream" (i.e., offshore, in the case of a coastal upwelling).

Fig. 11 shows the relationship between the linearity of equation (1), expressed by means of its coefficient of determination, and different values for reexpression (in %) of "half empty" and "half full". As might be seen, 40% for half empty and 60% for half full best linearizes equation (1), given the data at hand. Fig. 12 shows the resulting plot of transformed stomach contents and fullness index.

Fig. 13 and Table 5 summarize the results of the application of Sainsbury's model I (i.e., equations 5a, 5b and 5c) to the stomach content/fullness data in the Rojas de Mendiola/Alamo database.

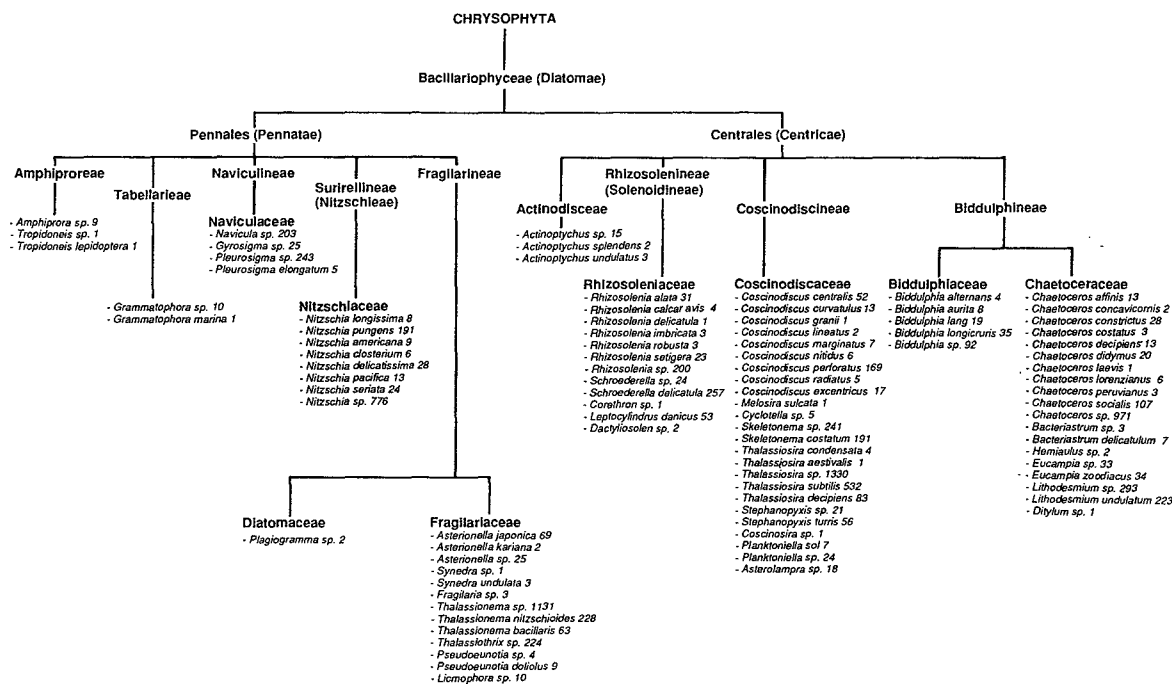


Fig. 8. Diatom species ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences, see also Fig. 5).  
 Fig. 8. Especies de diatomeas ingeridas por la anchoveta peruana, 1953 a 1982 (los números indican la ocurrencia, ver también Fig. 5).

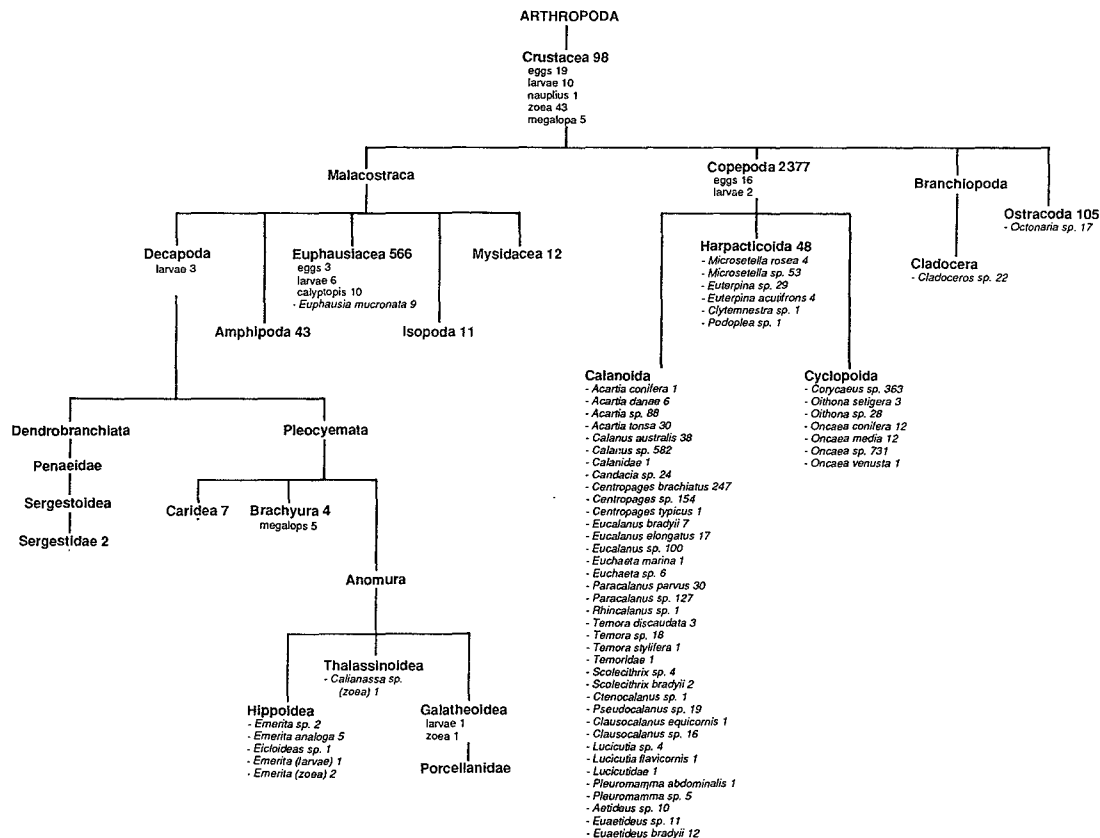


Fig. 9. Arthropod taxa ingested by Peruvian anchoveta, 1953 to 1982 (numbers indicate occurrences, see also Fig. 6).  
 Fig. 9. Artrópodos ingeridos por la anchoveta peruana, 1953 a 1982 (los números indican la ocurrencia, ver también Fig. 6).

Table 4. Results of test of comparison of the mean zooplankton fractions in Fig. 10 (see also text).

Tabla 4. Resultados del test de comparación de los promedios de las fracciones de zooplancton de la Fig. 10 (ver también texto).

Items tested	t	Degrees of freedom	Significant? ( $\alpha < 0.05$ )
<b>North/South</b>			
<10°S vs. 10-13°59'S	12.66	4,063	yes
<10°S vs. 14°S	9.27	3,924	yes
10-13°59'S vs. 14°S	3.32	4,487	yes
<b>Temperature</b>			
<17°C vs. 17-19.9°C	1.56	5,296	no
<17°C vs. $\geq 20^\circ\text{C}$	7.24	3,644	yes
17-19.9°C vs. $\geq 20^\circ\text{C}$	8.29	3,676	yes
<b>Time</b>			
<1975 vs. 1975-1978	5.99	4,613	yes
<1975 vs. 1979	3.04	3,842	yes
1975-1978 vs. 1979	9.33	4,022	yes
<b>Distance from shore</b>			
Inshore vs. intermediate	4.84	6,158	yes
Inshore vs. offshore	11.32	120	yes
Intermediate vs. offshore	9.36	133	yes

Information on stomach contents and exact sampling time were available for 5,245 individual anchoveta (mean wet weight 20.4 g); their mean sampling year was 1977 and their mean stomach content (as obtained by direct weighting or through conversion) are plotted as a function of time in Fig. 13, and further statistics are given on Table 5.

Sainsbury's model fitted these data extremely well (mean sum of squared residuals = 0.008), and this led to the following parameter estimates (all converted from relative to absolute stomach content):

- $a = 0.0340 \text{ g}\cdot\text{hour}^{-1}$ , i.e., an ingestion rate of  $0.034 \text{ g}\cdot\text{hour}^{-1}$  during the feeding period  
 $T_f = 10.92 \text{ hours}$ , i.e., anchoveta starts feeding at 10:55 a.m.  
 $T_m = 12.81 \text{ hours}$ , i.e., the feeding period is of 12.81 hours and lasts until 11:45 p.m.  
 and  $c = 0.1518 \text{ hours}^{-1}$ , i.e., anchoveta evacuate 15.2% of their stomach content per hour.

This leads to a daily ration estimate of  $R_d = 0.448 \text{ (g} \cdot \text{day}^{-1})$ , and hence a relative daily food consumption (% BWD) of 2.2%.

The mean growth rate, for anchoveta of 20.4 g live weight was computed based on  $W_\infty = 61 \text{ g}$ ,  $K = 1.05 \text{ year}^{-1}$  and  $t_0 = 0$  (i.e., using estimates of  $L_\infty$ ,  $K$  and  $t_0$  for 1977 in Palomares et al. 1987, and based on the conversion of  $L_\infty = 21 \text{ cm}$  to  $W_\infty$  using a mean condition factor of 0.661 based on the mean of the 12 monthly values given for 1977 in Tsukayama and Palomares 1987).

The resulting growth rate was  $dw/dt = 0.0772 \text{ g} \cdot \text{day}^{-1}$  and hence

$$K_1 = 0.0772/0.448 = 0.2075$$

which leads, given equation (10) to  $\beta = 0.173$ .

These parameter estimates, led, when used in conjunction with  $Z = 4.5 \text{ year}^{-1}$  (Pauly and Palomares, this vol.) and equation (11) to an estimate of  $Q/B = 3.30\%$  (daily), i.e., the anchoveta population would consume 12.1 times its own weight per year (at a mean SST of  $17.1^\circ\text{C}$ ).

These results correspond well with previous estimates obtained from metabolic studies. Palomares et al. (1987), based on Villavicencio (1981) and Villavicencio and Muck (1983a, 1983b, 1985), had estimated ration of adult anchoveta (in % BWD) to range between 3.50% ("1950" conditions) and 2.6% ("1980" conditions), thus bracketing our estimate of 3.30%/day.

Table 5. Data for the estimation of ration and feeding periodicity in anchoveta. (Source: Rojas/Alamo database, see text).

Tabla 5. Datos para la estimación de la ración alimenticia y periodicidad de alimentación de la anchoveta (fuente de información: base de datos de Rojas/Alamo, ver texto).

Time (hours)	n	Relative stomach content (% body weight)	Standard error (% body weight)	Observed stomach content <sup>a,b</sup> (g)	Estimated stomach content <sup>b</sup> (g)
0.75	50	1.32	0.133	0.191	0.1696
2.25	95	0.46	0.038	0.135	0.1351
3.75	76	0.21	0.018	0.074	0.1076
5.25	170	0.43	0.034	0.063	0.0857
6.75	484	0.29	0.013	0.068	0.0682
8.25	832	0.28	0.010	0.067	0.0543
9.75	773	0.41	0.015	0.074	0.0433
11.25	694	0.40	0.014	0.067	0.0516
12.75	379	0.17	0.003	0.051	0.0867
14.25	369	0.17	0.005	0.099	0.1146
15.75	373	1.11 <sup>a</sup>	0.054	0.177	0.1369
17.25	353	0.88	0.041	0.181	0.1546
18.75	216	0.68	0.025	0.173	0.1687
20.25	241	0.99	0.056	0.152	0.1799
21.75	53	0.57	0.076	0.177	0.1889
23.25	87	1.04	0.101	0.199	0.1960
Total	1,948			Mean 0.12175	

<sup>a</sup>Refers to an average body weight of 20.37 g calculated from 1,948 individual anchoveta and to a running average over three time intervals.

<sup>b</sup>See Fig. 13.

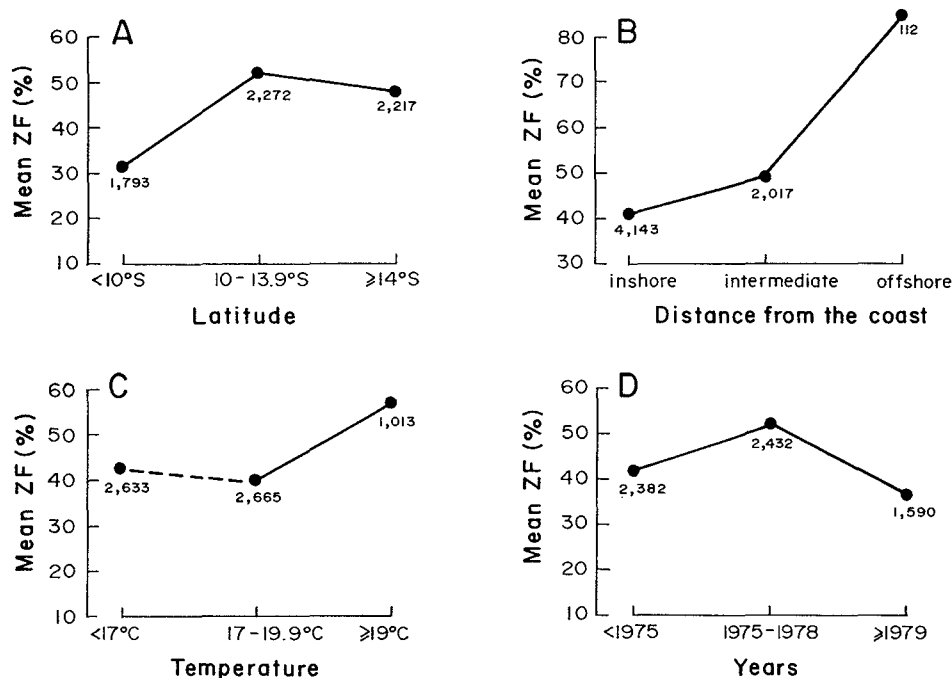


Fig. 10. Trends in zooplankton fraction (ZF) of anchoveta diet off Peru. The solid lines illustrate significant changes ( $P < 0.05$ ), while the dotted line links means that are not significantly different; the number of observations are given under each mean.

Fig. 10. Tendencias de la fracción de zooplankton (ZF) en la dieta de la anchoveta en la costa peruana. La línea sólida muestra cambios significativos ( $P < 0.05$ ), mientras que la línea entrecortada une promedios que no son significativamente diferentes; el número de observaciones se anotan debajo del promedio.

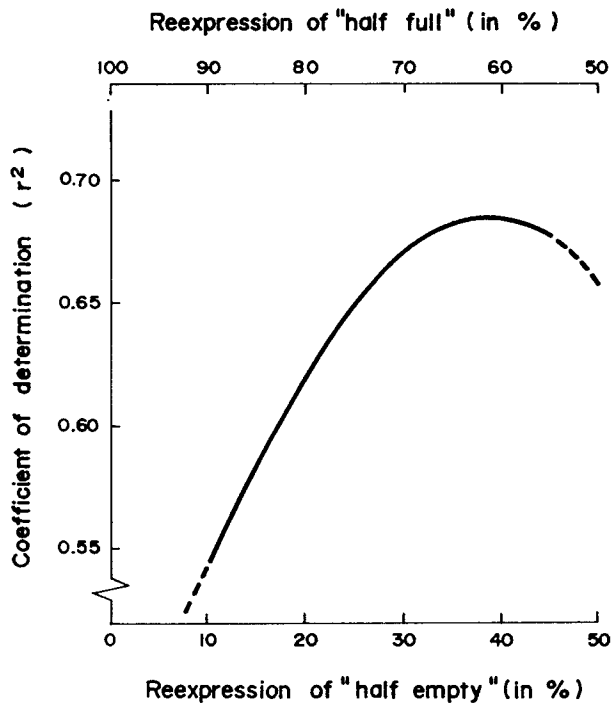


Fig. 11. Relationship between linearity of equation (1) - as expressed by the coefficient of determination - and different % values for the quantitative reexpression of "half empty" and "half full" as fullness indices of anchoveta stomach (see text and Rojas de Mendiola, this vol.).

Fig. 11. Relación entre la linealidad de la ecuación (1) - expresada por el coeficiente de determinación - y los diferentes valores porcentuales para la reexpresión cuantitativa de "semivacío" y "semilleno", como índice de llenura del estómago (contenido estomacal) de anchoveta (ver texto y Rojas de Mendiola, este vol.).

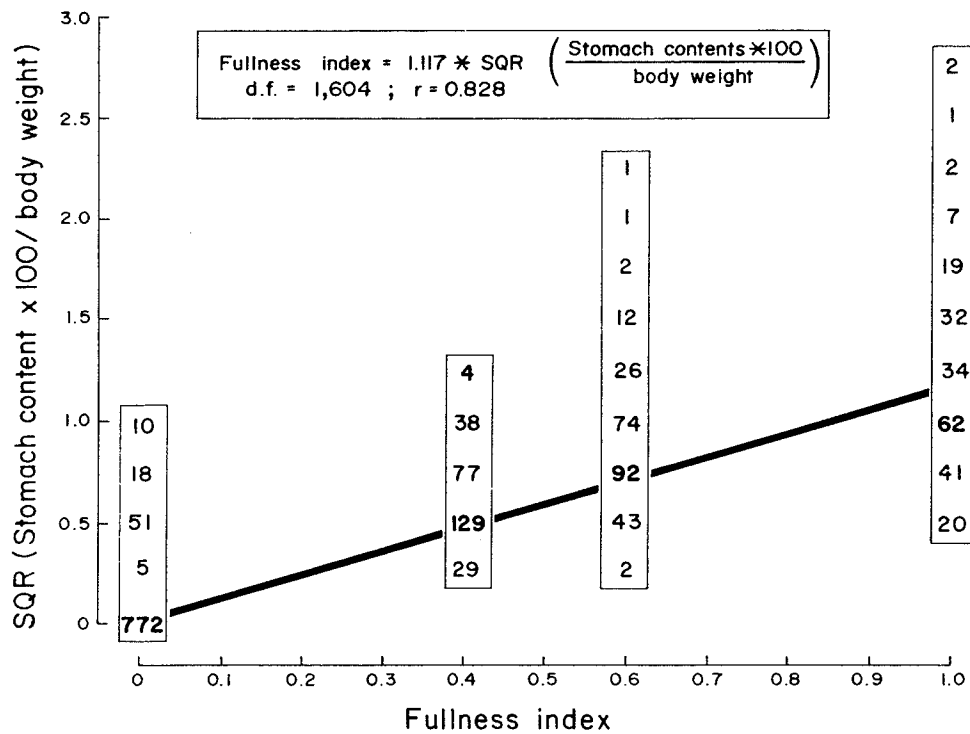


Fig. 12. Relationship between transformed stomach contents and their fullness index in 1,604 anchoveta for which pairs of values were available. Note linearity of relationship achieved by reexpression of "half empty" as 0.4 and "half full" as 0.6 (see text and Rojas de Mendiola, this vol.).

Fig. 12. Relación entre los contenidos estomacales transformados y su índice de llenura en 1,604 anchovetas en las que estuvieron disponibles pares de valores. Note la linealidad de la relación obtenida para la reexpresión de "semivacío" como 0.4 y para "semilleno" como 0.6 (ver texto y Rojas de Mendiola, este vol.).

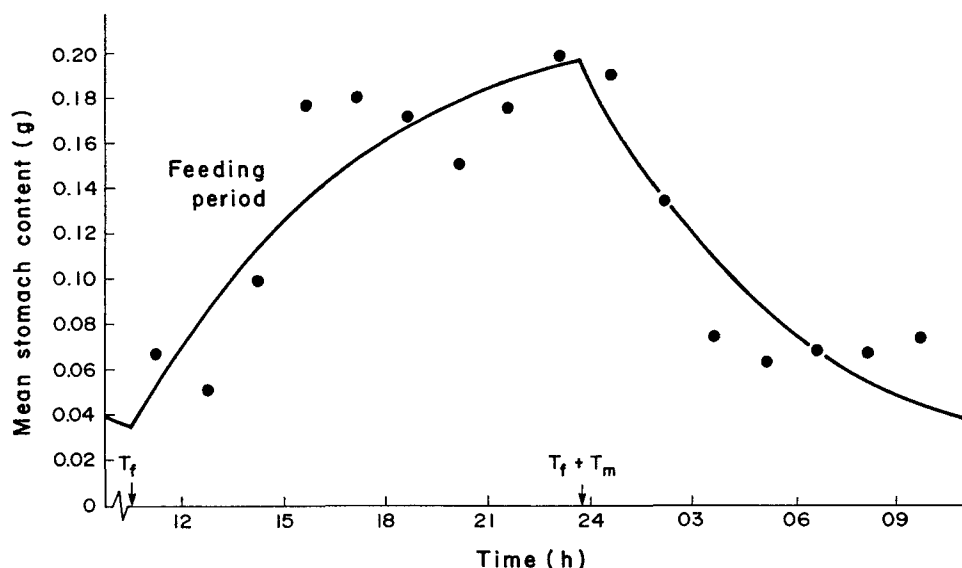


Fig. 13. Dynamics of stomach contents in Peruvian anchoveta, 1953 to 1982 ( $n = 5,245$ ). Note marked diurnal feeding cycle, with shape consistent with Sainsbury's (1986) feeding model (see also Table 5 and text).  
 Fig. 13. *Dinámica (cambios) del contenido estomacal de la anchoveta peruana, 1953 a 1982 ( $n = 5245$ ). Note se un marcado ciclo diurno de alimentación, compatible con el modelo de alimentación de Sainsbury (1986) (ver también Tabla 5 y texto).*

Tsukayama and Sanchez (1981), based on Villavicencio (1981), and on experiments in which they fed fish flesh to anchoveta, estimated a daily consumption of 4% BWD for anchoveta of 10 g.

Cushing (1978) suggested that "the daily ration as percentage of body weight for a fish as small as the anchoveta is likely to be nearer 5% than 1%. If the mean length were 12.5 cm, a reasonable daily ration would be equal to 0.66 ml, which is 10 times the weight of algae in the guts".

Equations (6) to (11), applied to Cushing's estimate of ration for 12.5 cm anchoveta (i.e., of 13 g), and assuming 1 ml = 1 g, the same growth and mortality as used above, leads to  $Q/B = 6.34\%/day$ . This is markedly higher than our estimate of 3.30%, and also higher than the estimate of 2.6 to 3.5% reported in Palomares et al. (1987). However, these lower estimates are based on mixed zoo- and phytoplankton diet (mean ZF for data used to estimate  $R_d = 49.6\%$ , see Villavicencio and Muck (1983a, 1983b, 1985)). If one assumed, with Brett and Groves (1979), that zooplankton provides about four times more net energy than the pure phytoplankton diet considered by Cushing (1978), one can estimate as  $Q/B = 3.95\%/day$  value, had he considered an equal proportion of zoo- and phytoplankton in the diet of anchoveta. This is close enough to our estimate, considering that it actually was a "guesstimate".

Our value of  $E_t = 0.373$  is, on the other hand, higher than the previously estimated "growth efficiency of 0.093 ("1950") to 0.239 ("1980", see Palomares et al. 1987), and also higher than the range of 0.10-0.20 used by Chavez et al. (this vol.). However, this high value is in line with Muck (this vol.) who suggests that anchoveta has a higher growth (i.e., trophic) efficiency than sardine, for which values of up to 0.185 have been proposed (Lasker 1973).

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