ANCHOVY EGG DISPERSAL AND MORTALITY AS INFERRED FROM CLOSE-INTERVAL OBSERVATIONS

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Kiil. Millions of tons of water come down that river. How do you know the day you made your tests there wasn't something unusual about the water?

Stockman. No, I took too many samples.

Kiil.How do you know? Why couldn't those little animals have clotted up only in the patch of water you souped out of the river? How do you know the rest of it wasn't pure?

Stockman. It's not probable . . . .

An Enemy of the People[1]

ABSTRACT

The oceanic boundary currents and continental borderlands that anchovy inhabit comprise diverse spatial and temporal scales of motion. Repetitive sampling at close intervals has been conducted to explore the sources and intensity of variance of observations and maximize the effectiveness of a management-oriented sampling program. The critical scale of repetitive sampling occurs when adjacent observations are so interdependent that they do not improve the precision of the abundance estimates. Sampling studies indicate that the scale of anchovy egg interdependence is on the order of several hundred meters for some days and somewhat less than this in the first few hours after spawning. Spatial correlation appears to diminish rapidly at scales larger than 2,000 m. The minimum distance between stations in the California egg production cruises is 7,500 m; in the Peru egg production survey it was 5,500 m.

In general, large structures in the ocean persist longer than small ones. One simple parameterization of this phenomenon is that a 600-m structure persists for 6 hours in the ocean and that structures of 2,800, 27,000, 147,000 m persist for a day, a week, and a month, respectively. From simple considerations, if the average value of food abundance is too low for larval fish to survive, the useful scale of oceanic feature that contains sufficient food is about 27 km if the food is required for a week, or 147 km if the food is required for a month. The critical scale of these features becomes smaller if production within the structure exceeds consumption and washout. The influence of persistence on survival may diminish as juveniles gain the ability to graze in schools and swim through larger intervening distances between favorable patches. We believe that experimental repetitive sampling supports the general scale for the passive dispersion of eggs: no obvious interrelations between interannual changes in these features and egg and larval survival were noted for the first 20 days of life. The consequences of a laterally incoherent and dissipated habitat may be delayed to the late larval and juvenile stages.

Will we be able to observe the later life stages with the same intensity and accuracy that we have observed the embryonic stages?

RESUMEN

Las corrientes oceánicas de margen y los aledaños continentales que habita la anchoveta sufren movimientos de diferentes escalas temporales y espaciales. Se condujeron muestreos replicados a intervalos reducidos con el fin de explorar las fuentes e intensidad de la varianza de las observaciones y maximizar la eficacia de un programa de muestreo orientado hacia el manejo del recurso. La escala crítica del muestreo repetitivo ocurre cuando las observaciones adyacentes son tan interdependientes que no aumentan la precisión de las estimaciones de abundancia. Muestreos experimentales indican que la escala de interdependencia para los huevos de la anchoveta es del orden de varios centenares de metros durante algunos días, y algo menor en las primeras horas después del desove. La correlación espacial parece disminuir rápidamente a escalas mayores de 2000 m. La distancia mínima entre estaciones en las campañas californianas de producción de huevos es de 7500 m; en los estudios peruanos de producción de huevos era de 5500 m. En general, las estructuras oceánicas mayores son más persistentes que las pequeñas. Una expresión cuantitativa sencilla de este fenómeno consiste en que estructuras de 600 m persisten en el océano durante 6 horas, mientras que aquéllas de 2,800, 27,000 y 147,000 m persisten durante un día, una semana, y un mes, respectivamente. Partiendo de consideraciones simples se deduce que si la abundancia promedio de alimento es demasiado baja para la supervivencia de las larvas

[1]Henrik Ibsen. *An Enemy of the People*. An adaptation for the American stage by Arthur Miller. Dramatists Play Service, Inc., New York, 1951.

de peces, la escala útil de la estructura oceánica que contiene alimento suficiente es de, aproximadamente, 27 km, si el alimento es requerido para una semana, o 147 km si lo es para un mes. La escala crítica de estas características disminuye si la producción dentro de la estructura excede al consumo y la exportación. La influencia de esta persistencia en la supervivencia puede disminuir a medida que los juveniles van adquiriendo la capacidad de alimentarse en cardúmenes y de nadar distancias mayores entre lugares favorables. Creemos que el muestreo repetitivo experimental concuerda con la escala general de dispersión pasiva de los huevos: no se observaron interrelaciones obvias entre cambios interanuales en estas características y la supervivencia de huevos y larvas durante los primeros 20 días de vida. Las consecuencias de un hábitat lateralmente incoherente y disipado pueden ser pospuestas hasta los estados larvales avanzados y los juveniles.

¿Podremos observar los estados de desarrollo tardíos con al misma intensidad y precisión con que observamos los estados embrionarios?

INTRODUCTION

Demands on oceanic sampling have rapidly increased from the simple detection and description of resources (Ahlstrom 1968; Hempel 1973; Smith and Richardson 1977) to the testing of hypotheses on the causes of recruitment failure in dynamic coastal areas like the California Current (Lasker 1975; Vlymen 1977; Parrish and MacCall 1978; Lasker and Zweifel 1978; Parrish et al. 1981; Smith 1981; Hewitt 1981; Bakun and Parrish 1982). Smith (1981) described sampling strategies for testing several hypothesized sources of year-class failure; the sources include larval transport, critical period, predation including cannibalism, starvation, unfavorable distribution pattern, and parental deficiencies at the time of spawning. Success in the studies underway have encouraged international organizations (Bakun et al. 1982) to compare dynamic areas like the eastern boundaries of the oceans off South America and Africa with respect to the causes of massive fluctuations in fish reproductive success. These studies require additional work on efficient delineation of distribution and biomass estimation. Because of the nature of the survival mechanisms postulated, directed work on spatial pattern, turbulent diffusion, transport, and survival is also needed.

The spatial pattern of plankton may be considered from the aspects of interpreting existing samples and the strategy of future sampling (Silliman 1946; Sette and Ahlstrom 1948; Taft 1960; Zweifel and Smith 1981). Another aspect of spatial pattern of plankton is the interaction between predator and prey, in particular where food aggregations are necessary for sufficient feeding rates (Lasker 1975; Vlymen 1977; Lasker and Zweifel 1978; Hewitt 1981). Lastly, schooling coastal pelagic fishes proceed through a planktonic phase of weeks to months, and the eventual retention of viable concentrations of juveniles near the coast may be controlled by rates of turbulent diffusion and cross-shelf transport during the spawning season (Smith 1973; Smith and Lasker 1978; Parrish and MacCall 1978; Hewitt 1982; Bakun and Parrish 1982; Smith 1985).

The scale of spatial pattern contains additional information about the recent history and near future of the pelagic aggregation. For example, if individual (0.3 m) spawning pelagic fish like sardines are found in populations (1,000 km), school groups (10 km), schools (100 m), and spawning "cliques" (30 m), one can infer from the rate of dispersal by turbulent diffusion that the major sources of variance in samples are from individuals, cliques, and schools rather than from school groups and populations based on the length-scale assumptions (Smith 1973). Since this pattern of eggs imposed by the spawning and fertilization behavior of the adults persists several days into the larval stage, one may postulate that similar features like diatom patches or grazed gaps in diatom layers would persist equally long in the pelagic environment (Okubo 1971).

It is the purpose of this symposium to explore similarities among the eastern boundary areas of the world oceans, because these contain the potential of tens of millions of tons annual catch of schooling coastal pelagic engraulids, clupeids, scombrids, and carangids. These fisheries are generally not managed and are subject to large natural fluctuations, which seem to be augmented by present fishing practices (Murphy 1977; Smith 1981; Bakun and Parrish 1982; Lasker 1985; Smith 1985). Our objective in this paper is to present a small-scale empirical study of anchovy egg dispersal in a coastal site. The study may then be considered in the context of large-scale environmental features and biological surveys. We believe that existing techniques can be modified to measure offshore drift and dispersal within the coastal habitat and thus describe the habitat of schooling coastal pelagic fish in eastern boundary habitats.

METHODS

The methods used for close-interval sampling of the anchovy population off California are described in detail in Lasker (1984), Smith and Hewitt (1984), Smith, Flerx, and Hewitt (1984) and Moser and Ahlstrom (1984). We will only briefly describe the planning and conduct of the cruise, station activity, the

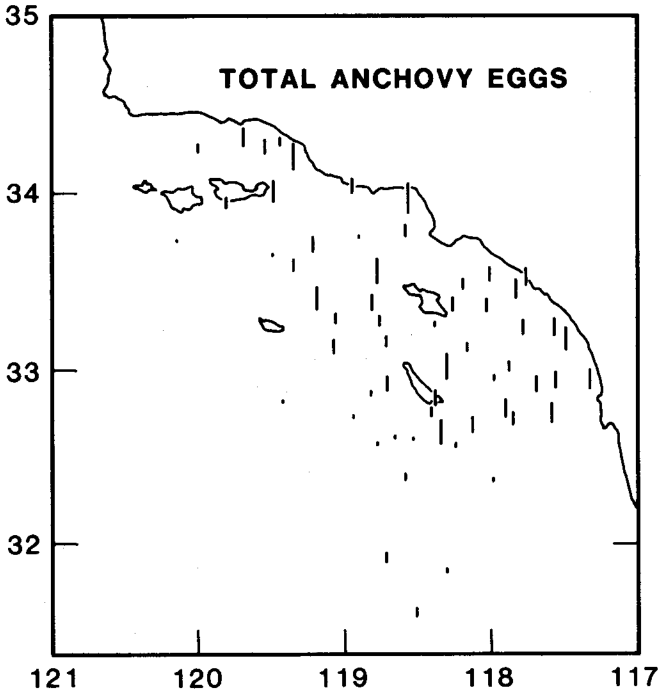

Figure 1. The survey area off southern California. Ordinate values are degrees north latitude, and the abscissa values are degrees west longitude. The lengths of the bars are proportional to the log of the number of anchovy eggs per 0.05 square meters as an average of eight replicates at each station. (See Table 5 for data.)

net, the procedures for sorting, staging and aging the eggs, and the data analysis.

Cruise

The cruise was planned to encompass the spawning habitat of the central population of the northern anchovy (*Engraulis mordax*) with groups of eight samples at stations 20 miles apart in the cross-shelf direction and 40 miles apart parallel to the general run of the coast. Unfortunately, the 25-m motor vessel (*Scorpius*) chartered for this cruise was not competent to occupy the preplanned stations in the weather of January 1979; therefore, stations in the general area of the spawning were occupied at haphazard positions that could be approached from safe harbors among the islands of the Southern California Bight. The stations that had at least one egg in eight tows are plotted in Figure 1 as "sticks" with height proportional to the log of the mean number of total anchovy eggs per observation.

On station we recorded position, cast a 10-m Nansen bottle with reversing thermometer to estimate the temperature, and made eight vertical plankton tows to a wire length of 70 m and back. The positions, date, and time of arrival at the station and the 10-m temperature are listed in Appendix Table 1. To maintain position on the station (relative to the water) as closely as possible, the officers of the vessel were instructed to keep the 45-kg weight on 10-m, 3/16″ cable vertical between casts and tows for the entire duration of the station. The usual interval between vertical tows was 12 minutes, but occasionally repeat tows and delays between tows lengthened that period. The distribution of intervals between adjacent tows is depicted in a histogram in Appendix Table 2; this average interval will be used to interpret all tows.

The Tow

Of the 12 minutes between the initiation of tows, 3-5 minutes were involved with lowering and raising the net, another 5 minutes was required to wash the net and concentrate the sample in the cod end, and 4-5 minutes was needed to preserve the sample in Formalin and label the sample bottle. The winch on the charter vessel was incapable of obtaining the 70-m-per-minute towing rate specified for the project, and rates were commonly in the range of 25 to 40 m per minute.

The plankton net was based on the original design of anchovy egg net (Smith et al. 1968) and modified for vertical towing (Hewitt 1983; Smith et al. 1984). As the original net in the vertical tow series, it differed from the present design by being a single net, with mesh aperture area of 0.333-mm nylon mesh. The mesh-aperture-to-mouth-aperture ratio was 8.7:1, of which 35% was in the terminal conical portion of the net and 65% was in the cylindrical portion to reduce length and facilitate self-cleaning under tow. Nets were washed from the outside by a moderate rate of flow.

Laboratory Work

Anchovy eggs were sorted from samples with a dissecting microscope at a magnification of about 10 × (Kramer et al 1972; Smith and Richardson 1977). The sorted eggs were subsequently staged using criteria of Moser and Ahlstrom (1984). Ages were estimated from the temperature-specific stage development rate (Ahlstrom 1943; Zweifel and Lasker 1976; Lo 1984), the actual time of tow, and the 10-m temperature on the station.

Data Analysis

Descriptive statistics were performed on the UCSD-VAX using Minitab. A correlation matrix on all ages of egg for all 60 tows was performed, yielding 7 correlation coefficients for adjacent columns, 6 for tows 24 minutes apart, 5 for tows 36 minutes apart, etc. Negative binomial parameter estimates were accomplished using the iterative techniques described in Southwood (1978). The BASIC program implemented on the UCSD-VAX to estimate the negative binomial parameters is listed in the Appendix.

TABLE 1
Replicate Observations of Anchovy Eggs < One Day Old

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	1	2	4	9	23	3	15	64	15.125
2	0	0	1	0	0	0	1	0	0.250
3	0	0	0	0	0	2	3	17	2.750
4	4	5	0	8	7	8	10	12	6.750
5	0	0	0	0	0	0	0	0	0.000
6	4	2	7	0	0	0	0	0	1.625
7	0	0	0	0	0	0	0	0	0.000
8	1	0	0	0	0	0	0	0	0.125
9	0	0	0	0	0	0	0	0	0.000
10	0	0	0	0	0	0	0	0	0.000
11	1	0	0	0	1	0	1	0	0.375
12	0	0	0	0	1	3	0	5	1.125
13	0	0	0	0	0	0	0	0	0.000
14	0	0	0	0	0	0	0	0	0.000
15	30	39	51	0	0	0	0	0	15.000
16	0	0	0	0	0	0	0	0	0.000
17	0	0	0	0	0	0	0	1	0.125
18	0	0	0	0	0	0	0	0	0.000
19	13	6	20	6	4	6	0	0	6.875
20	0	0	0	0	0	0	0	0	0.000
21	0	0	0	0	0	0	0	0	0.000
22	0	0	0	0	0	0	0	0	0.000

RESULTS

We will consider three aspects of the data. The first will be the data set itself. Secondly, we will describe the data and a possible probability-generating distribution from which it may have been drawn. Thirdly, we will consider one interpretation of the change of the data with time.

The Data Set

The data set consists of four ages of egg, and the distribution of total eggs. The four ages of egg are those eggs less than 8 hours old, 1 day old, 2 days old, and 3 days old. These sets are from the same 8 replicates of 60 observations containing at least one anchovy egg per station.

Eggs produced in the first 8 hours after the onset of spawning are considered separately in the analysis of egg production because incidence and abundance are underestimated. (Smith and Hewitt 1984) In Table 1, it may be seen that of the 60 samples considered, only 22 were in the initial 8-hour period. In no case does a large sample observation continue across the entire set of eight observations on the station. For example, in row 1, replicates 5, 7, and 8 indicate that the ship drifted into a patch, whereas rows 15 and 19 indicate that the ship drifted out of a patch.

The chief difference for one-day-old eggs (Table 2) is that in most observations, the set of replicates is usually taken entirely within or outside of a patch. There are still instances, such as row 49, that indicate drifting out, but most show moderate changes within replicates on station. There are no visible differences in Tables 3 or 4 from Table 2 in terms of continuity of observations on station.

TABLE 2
Replicate Observations of Anchovy Eggs One Day Old

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	3	3	3	6	2	2	1	3	2.875
2	2	1	3	4	3	3	0	5	2.625
3	8	5	7	7	6	10	5	13	7.625
4	0	0	0	0	0	0	0	0	0.000
5	0	0	0	0	0	0	0	0	0.000
6	0	1	2	0	4	2	1	2	1.500
7	12	10	10	6	5	3	4	6	7.000
8	5	1	6	6	4	2	10	5	4.875
9	0	0	0	2	0	0	0	1	0.375
10	0	0	0	0	0	0	0	0	0.000
11	9	3	2	2	0	0	3	0	2.375
12	12	23	12	4	7	5	7	5	9.375
13	0	1	0	2	3	3	1	1	1.375
14	0	1	0	0	1	2	0	0	0.500
15	2	5	2	3	0	1	2	0	1.875
16	6	8	3	6	2	6	4	5	5.000
17	3	3	1	2	3	2	0	4	2.250
18	2	0	1	0	1	2	2	2	1.250
19	18	26	21	33	21	32	22	23	24.500
20	0	0	0	0	0	0	0	0	0.000
21	1	3	3	3	2	0	1	0	1.625
22	2	2	9	5	4	4	9	8	5.375
23	0	1	1	1	0	1	3	1	1.000
24	0	0	0	0	0	0	0	0	0.000
25	0	0	0	0	0	0	0	0	0.000
26	0	0	0	0	0	0	0	0	0.000
27	1	0	0	1	0	4	5	1	1.500
28	2	1	0	0	0	0	1	1	0.625
29	4	2	5	0	3	3	0	4	2.625
30	15	5	13	16	10	13	12	6	11.250
31	14	12	11	11	9	7	8	5	9.625
32	0	0	2	1	0	0	0	0	0.375
33	0	0	0	0	0	0	0	0	0.000
34	0	0	0	1	0	0	1	0	0.250
35	2	0	0	1	0	1	0	0	0.500
36	1	2	0	3	0	0	0	0	0.750
37	0	0	0	0	0	0	1	0	0.125
38	17	11	22	26	37	27	20	30	23.750
39	5	8	12	4	6	4	3	3	5.625
40	3	2	3	2	0	3	3	1	2.125
41	0	1	0	2	2	0	0	1	0.750

(continued)

TABLE 2 (continued)

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
42	0	0	0	0	0	0	0	0	0.000
43	0	1	0	0	0	0	0	1	0.250
44	1	4	0	3	5	3	4	3	2.875
45	7	4	4	1	3	2	2	3	3.250
46	0	0	0	0	0	0	0	1	0.125
47	1	1	2	1	1	3	1	5	1.875
48	0	0	0	0	0	0	0	0	0.000
49	3	22	3	0	0	0	0	0	3.500
50	0	0	0	0	0	0	0	0	0.000
51	0	0	1	0	0	0	0	0	0.125
52	0	0	0	0	0	0	0	0	0.000
53	0	0	0	0	0	0	0	0	0.000
54	5	4	3	0	3	2	2	3	2.750
55	0	0	1	0	2	0	0	0	0.375
56	1	2	3	2	4	3	3	4	2.750
57	64	65	64	63	48	82	54	48	61.000
58	1	0	0	2	1	1	5	3	1.625
59	11	20	5	20	20	12	22	18	16.000
60	5	10	8	5	5	7	4	7	6.375

TABLE 3
Replicate Observations of Anchovy Eggs Two Days Old

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
1	0	1	0	1	0	2	1	1	0.750
2	0	2	0	1	1	1	1	1	0.875
3	0	1	2	0	1	1	0	1	0.750
4	2	0	2	1	1	0	2	1	1.125
5	0	2	1	1	3	0	1	3	1.375
6	3	5	5	6	8	15	14	12	8.500
7	2	2	0	4	2	2	1	0	1.625
8	6	12	11	8	12	9	10	9	9.625
9	0	0	0	0	0	0	0	0	0.000
10	0	0	0	0	0	0	0	0	0.000
11	0	0	0	0	0	1	0	0	0.125
12	0	0	0	0	0	0	0	0	0.000
13	1	1	3	0	0	0	3	2	1.250
14	2	3	5	0	6	7	4	10	4.625
15	1	2	2	0	4	2	1	2	1.750
16	5	2	6	2	2	1	3	2	2.875
17	0	0	0	2	4	4	4	4	2.250
18	1	1	2	0	1	1	1	2	1.125
19	6	14	11	12	12	9	5	9	9.750
20	1	2	2	1	0	3	1	1	1.375
21	7	5	7	2	2	5	1	5	4.250
22	26	32	46	30	17	9	14	13	23.375
23	1	2	2	2	0	0	2	0	1.125

(continued)

TABLE 3 (continued)

	Replicate Number								
Row	1	2	3	4	5	6	7	8	Average
24	0	0	0	0	0	0	0	1	0.125
25	0	0	0	1	0	0	0	0	0.125
26	0	0	0	0	1	0	0	0	0.125
27	1	0	6	4	2	2	10	3	3.500
28	3	2	6	4	1	0	3	6	3.125
29	34	35	40	30	36	39	35	35	35.500
30	7	3	1	2	3	4	1	7	3.500
31	22	10	13	11	15	21	9	12	14.125
32	3	3	2	3	3	3	3	0	2.500
33	0	0	0	0	0	0	0	0	0.000
34	4	1	1	3	1	0	0	0	1.250
35	0	0	0	0	0	0	0	0	0.000
36	0	1	0	0	0	0	0	0	0.125
37	2	0	1	0	0	0	0	0	0.375
38	5	4	3	15	21	15	9	13	10.625
39	0	0	0	0	0	0	0	0	0.000
40	3	3	1	0	2	0	2	3	1.750
41	0	0	0	0	0	0	0	0	0.000
42	1	0	0	0	0	0	0	0	0.125
43	1	1	0	1	0	0	1	2	0.750
44	4	4	9	5	2	8	2	11	5.625
45	0	0	0	0	0	3	2	2	0.875
46	0	0	0	0	0	0	1	1	0.250
47	39	21	39	21	18	48	16	22	28.000
48	0	0	0	0	0	1	0	0	0.125
49	0	2	1	0	2	0	2	0	0.875
50	6	4	4	10	7	4	8	5	6.000
51	2	4	6	4	1	2	4	2	3.125
52	0	0	0	0	0	0	0	0	0.000
53	0	0	0	0	0	0	0	0	0.000
54	27	22	21	0	8	11	4	4	12.125
55	0	0	0	0	0	0	0	0	0.000
56	22	14	6	9	6	4	6	1	8.500
57	96	117	94	89	84	119	111	91	100.125
58	12	3	9	6	3	4	5	9	6.375
59	8	6	2	4	4	2	9	5	5.000
60	1	5	6	4	4	5	12	10	5.875

Table 5 contains the values for all ages of anchovy egg within each station set. At these temperatures, one may expect three ages of egg within close proximity. In this set, only rows 33, 52, and 53 had none of the three ages identified: row 10 had neither one- nor two-day-old eggs, row 35 had neither two- nor three-day-old eggs, and rows 24, 26, 42, and 50 had neither one- nor three-day-old eggs.

In summary, there is coherence among the replicate stations of anchovy eggs older than eight hours. This indicates that the scale of the pattern is large relative to the drift of the research vessel and the layers of water below over periods of one to two hours.

TABLE 4
Replicate Observations of Anchovy Eggs Three Days Old

Row	Replicate Number 1	2	3	4	5	6	7	8	Average
1	0	0	0	0	0	0	0	0	0.000
2	0	0	0	0	0	0	0	0	0.000
3	3	4	4	2	1	3	0	2	2.375
4	1	0	4	3	3	1	0	2	1.750
5	3	4	5	4	4	4	1	11	4.500
6	3	0	2	1	2	2	2	2	1.750
7	2	6	9	4	3	3	3	2	4.000
8	1	1	5	2	3	5	5	5	3.375
9	0	0	0	0	0	0	0	0	0.000
10	0	0	0	0	0	0	0	1	0.125
11	5	4	0	3	1	1	4	9	3.375
12	9	11	8	5	8	1	5	5	6.500
13	1	2	2	1	1	3	3	2	1.875
14	2	4	5	3	2	7	2	4	3.625
15	1	0	1	0	0	0	0	1	0.375
16	8	5	3	5	10	6	8	3	6.000
17	9	3	3	0	1	0	1	1	2.250
18	1	0	3	0	1	0	3	0	1.000
19	17	16	15	20	10	10	11	5	13.000
20	4	5	8	4	3	7	5	2	4.750
21	13	7	6	4	9	7	7	3	7.000
22	24	16	16	10	8	9	4	6	11.625
23	1	3	1	2	0	4	1	2	1.750
24	0	0	0	0	0	0	0	0	0.000
25	0	3	0	0	0	0	0	0	0.375
26	0	0	0	0	0	0	0	0	0.000
27	5	0	9	6	6	5	11	10	6.500
28	1	1	0	1	1	0	1	0	0.625
29	21	17	15	23	14	11	14	17	16.500
30	20	6	18	22	9	11	3	9	12.250
31	6	4	5	4	5	2	7	1	4.250
32	1	0	0	1	0	1	1	0	0.500
33	0	0	0	0	0	0	0	0	0.000
34	0	0	1	0	0	1	0	0	0.250
35	0	0	0	0	0	0	0	0	0.000
36	0	0	0	0	0	0	0	0	0.000
37	0	1	1	1	1	0	0	0	0.500
38	3	4	5	4	3	2	4	5	3.750
39	0	0	0	0	0	0	0	0	0.000
40	0	0	0	1	0	0	1	1	0.375
41	0	0	0	0	0	0	0	0	0.000
42	0	0	0	0	0	0	0	0	0.000
43	4	8	4	7	8	5	3	11	6.250
44	2	5	5	2	5	5	6	12	5.250
45	0	1	0	0	1	0	2	2	0.750
46	0	0	0	0	2	1	2	0	0.625
47	25	29	32	43	41	53	52	45	40.000
48	1	2	4	1	0	1	1	0	1.250
49	1	1	0	0	0	0	0	0	0.250
50	0	0	0	0	0	0	0	0	0.000

(continued)

TABLE 4 (continued)

Row	Replicate Number 1	2	3	4	5	6	7	8	Average
51	61	69	75	84	76	62	61	68	69.500
52	0	0	0	0	0	0	0	0	0.000
53	0	0	0	0	0	0	0	0	0.000
54	10	10	12	0	5	8	2	5	6.500
55	120	86	119	107	136	114	104	102	111.000
56	0	0	0	0	0	0	0	0	0.000
57	22	26	16	34	16	28	42	26	26.250
58	1	2	2	6	1	5	3	3	2.875
59	3	8	5	2	6	3	3	3	4.125
60	7	12	12	14	9	12	15	17	12.250

TABLE 5
Replicate Observations of Anchovy Eggs All Ages Plus Disintegrated

Row	Replicate Number 1	2	3	4	5	6	7	8	Average
1	4	6	7	16	25	7	17	68	18.750
2	2	3	3	5	4	4	1	6	3.500
3	14	11	13	10	8	14	5	16	11.375
4	4	0	8	5	4	1	4	3	3.625
5	3	6	6	6	7	4	2	14	6.000
6	6	6	9	7	14	19	17	16	11.750
7	16	18	19	14	10	10	11	25	15.375
8	17	19	22	24	26	24	35	31	24.750
9	0	0	0	2	0	0	0	1	0.375
10	0	0	0	0	0	1	0	2	0.375
11	15	7	2	5	1	2	7	10	6.125
12	21	34	21	9	16	5	12	10	16.000
13	2	4	7	4	4	11	8	8	6.000
14	4	8	10	3	9	16	6	14	8.750
15	4	7	5	4	4	3	3	3	4.125
16	19	15	12	13	14	13	15	10	13.875
17	19	9	13	7	15	7	5	11	10.750
18	9	9	18	12	8	13	10	7	10.750
19	56	74	63	74	53	64	48	44	59.500
20	6	7	12	6	3	11	7	3	6.875
21	22	15	16	9	13	12	9	8	13.000
22	57	58	76	50	32	27	30	30	45.000
23	2	6	7	5	0	10	7	4	5.125
24	0	0	0	0	0	0	0	1	0.125
25	1	3	0	2	0	0	0	0	0.750
26	0	0	0	0	1	0	0	0	0.125
27	8	14	15	11	9	11	27	14	13.625
28	9	6	6	5	3	0	6	7	5.250
29	59	54	60	54	53	54	50	58	55.250
30	42	15	32	37	22	28	20	22	27.250
31	42	26	29	26	30	33	24	23	29.125
32	4	3	5	6	4	4	4	5	4.375
33	3	0	0	2	1	0	1	0	0.875

(continued)

TABLE 5 (continued)

Row	Replicate Number 1	2	3	4	5	6	7	8	Average
34	4	1	2	4	1	1	1	0	1.750
35	2	0	0	1	0	1	0	0	0.500
36	1	3	0	3	1	4	3	2	2.125
37	2	1	2	1	1	0	1	0	1.000
38	56	58	81	48	64	49	34	50	55.000
39	5	8	12	4	6	4	3	3	5.625
40	6	5	4	3	2	3	6	6	4.375
41	0	1	0	2	2	0	0	1	0.750
42	1	0	0	0	0	0	0	0	0.125
43	5	10	4	8	8	5	4	14	7.250
44	7	13	14	10	12	16	12	26	13.750
45	20	11	24	7	8	11	6	7	11.750
46	0	1	2	1	2	3	4	2	1.875
47	66	52	73	65	60	104	72	73	70.625
48	1	2	4	1	0	2	2	0	1.500
49	4	25	4	4	8	4	4	1	6.750
50	6	4	4	10	7	4	8	5	6.000
51	63	73	82	88	77	64	65	70	72.750
52	1	0	0	0	0	0	0	0	0.125
53	0	0	1	0	0	0	0	1	0.250
54	47	39	43	1	18	23	9	13	24.125
55	120	87	122	109	138	116	104	102	112.250
56	23	16	9	11	10	8	10	6	11.625
57	182	208	174	187	148	229	208	165	187.625
58	15	6	11	16	8	10	13	16	11.875
59	29	39	13	27	31	20	37	29	28.125
60	13	27	27	23	19	24	32	34	24.875

Data Summary

Owing to the wide range of numbers of eggs per sample, Tables 6, 7, and 8 are divided into classes whose boundaries encompass factors of four rather than unit frequencies. The general appearance of similarity among the replicate sets above is confirmed in the data summary table and the parameters calculated from them. The primary difference among the distributions of the eight replicates and the distribution of the mean of eight is the lower threshold (0.125 rather than 1 per .05 m^2) for the mean of eight samples on a station. Whereas one would expect the mean of the means to be the same as the mean of the replicates, one would expect the variance of the observations to be eight times the variance of the means of eight; instead, the variance of the means of eight is indistinguishable from the variances of the individual sets for one-, two- and three-day-old eggs.

The estimates of the negative binomial factor k are the same from replicate to replicate and between the means of eight and the eight replicates (Tables 6, 7, and 8).Thus the estimation of the negative binomial parameters, mean, and k from small sets of observations with high variance is relatively robust when small sample sizes are used. Furthermore, the negative binomial k is well estimated from the fraction of zero observations, and even the "moments" estimate (from the mean and variance) is reasonably close to the others and relatively stable under these conditions.

The distribution of the total eggs (Table 9) differs

TABLE 6
Anchovy Egg Sample Frequency Distribution
One-Day-Old Eggs

Eggs/0.05 m2	Replicate Number 1	2	3	4	5	6	7	8	Mean
0	26	24	27	25	29	27	27	25	13
0.0625 – 0.25	—	—	—	—	—	—	—	—	3
0.25 – 1	—	—	—	—	—	—	—	—	10
1 – 4	17	19	18	19	15	20	17	17	20
4 – 16	14	12	12	11	12	10	12	14	10
16 – 64	2	4	2	5	4	2	4	4	4
64 – 256	1	1	1	—	—	1	—	—	—
Mean	4.1	4.6	4.1	4.3	3.9	4.3	3.8	3.9	4.1
Variance	83.5	99.0	85.9	97.8	70.7	136.9	69.1	64.2	81.4
Neg. binomial									
$k(0)$	.321	.274	.277	.260	.283	.269	.327	.285	.312
$k(1)$	.158	.195	.163	.157	.118	.145	.155	.170	.202
$k(2)$	.264	.256	.254	.217	.234	.237	.252	.244	.296

$k(0)$ is the parameter of the negative binomial distribution as estimated from the proportion of '0' values.
$k(1)$ is the parameter of the negative binomial distribution as estimated from the sample mean and variance ('moments' estimate).
$k(2)$ is the maximum likelihood estimator (Southwood 1966).

TABLE 7
Anchovy Egg Sample Frequency Distribution
Two-Day-Old Eggs

	Replicate Number								
Eggs/0.05 m2	1	2	3	4	5	6	7	8	Mean
0	24	22	24	27	24	26	20	22	10
0.0625 – 0.25	—	—	—	—	—	—	—	—	7
0.25 – 1	—	—	—	—	—	—	—	—	8
1 – 4	18	21	16	14	19	15	21	18	17
4 – 16	11	12	15	15	12	15	16	17	14
16 – 64	6	4	4	3	4	3	2	2	3
64 – 256	1	1	1	1	1	1	1	1	1
Mean	6.1	5.9	6.3	5.0	5.0	6.1	5.4	5.4	5.7
Variance	213.2	265.7	222.0	163.8	148.8	292.4	225.0	163.8	198.8
Neg. binomial									
$k(0)$	.299	.347	.295	.268	.329	.262	.417	.363	.318
$k(1)$	.180	.134	.184	.157	.174	.130	.133	.184	.157
$k(2)$	.248	.276	.255	.241	.301	.227	.327	.316	.280

$k(0)$ is the parameter of the negative binomial distribution as estimated from the proportion of '0' values.
$k(1)$ is the parameter of the negative binomial distribution as estimated from the sample mean and variance ('moments' estimate).
$k(2)$ is the maximum likelihood estimator (Southwood 1966).

from that of any of the individual nights' spawning. In the individual age groups the frequency of observations decreases from the "0" class to the "64-256" eggs per observation class. In the total eggs observations, the frequency increases from the "0" class to the "4-16" class and then descends. Even when each station has at least one egg in eight samples, the number of observations with "0" eggs in each of the replicates varied from 10% to 18%.

We concluded that nearly uniform results would have been obtained from any set of replicates. Also, the frequency distribution of the total is a composite of the day-class observations and may in fact exhibit a different type of distribution when three days' egg

TABLE 8
Anchovy Egg Sample Frequency Distribution
Three-Day-Old Eggs

	Replicate Number								
Eggs/0.05 m2	1	2	3	4	5	6	7	8	Mean
0	22	25	24	25	24	25	23	24	15
0.0625 – 0.25	—	—	—	—	—	—	—	—	1
0.25 – 1	—	—	—	—	—	—	—	—	10
1 – 4	19	11	10	15	17	14	19	17	13
4 – 16	11	17	20	13	15	17	14	13	16
16 – 64	7	5	4	5	2	3	3	4	3
64 – 256	1	2	2	2	2	1	1	2	2
Mean	7.0	6.4	7.3	7.3	6.9	6.7	6.7	6.8	6.9
Variance	316.8	216.1	334.9	346.0	412.1	316.8	295.8	278.9	302.8
Neg. binomial									
$k(0)$	.321	.274	.277	.260	.283	.269	.327	.285	.283
$k(1)$	.158	.195	.163	.157	.118	.145	.155	.170	.157
$k(2)$	.264	.256	.254	.217	.234	.237	.252	.244	.257

$k(0)$ is the parameter of the negative binomial distribution as estimated from the proportion of '0' values.
$k(1)$ is the parameter of the negative binomial distribution as estimated from the sample mean and variance ('moments' estimate).
$k(2)$ is the maximum likelihood estimator (Southwood 1966).

TABLE 9
Anchovy Egg Sample Frequency Distribution
All Ages Plus Disintegrated

	Replicate Number								
Eggs/0.05 m2	1	2	3	4	5	6	7	8	Mean
0	7	10	11	6	10	11	10	9	—
0.0625 – 0.25	—	—	—	—	—	—	—	—	4
0.25 – 1	—	—	—	—	—	—	—	—	7
1 – 4	12	9	6	12	11	9	9	12	7
4 – 16	21	24	25	27	23	23	25	20	26
16 – 64	17	13	12	10	12	12	12	14	12
64 – 256	3	4	6	5	4	5	4	5	4
Mean	19.1	18.9	20.1	17.8	17.1	18.5	17.1	18.3	18.4
Variance	979.7	1049.8	1049.8	1004.9	852.6	1303.2	1024.0	829.4	961.0

production is present. This may be expected to differ for eggs that hatch in a day or persist for weeks.

Interpretation of Time Series

The correlation between recent observations of newly spawned eggs ends at intervals greater than 24 minutes, whereas one-day-old eggs have a persistent correlation over the entire 84-minute interval between the first and eighth tows (Figure 2). The coherence among tows increases gradually with the age of eggs. Coefficients of correlation over .24, or coefficients of determination over .06 are significant with 60 observations.

The time and space scales of controlled ship's drift in 1-2 hours are small in comparison with the change of distribution of a patch of eggs more than one day old. The scale of deposition of the eggs and their subsequent dispersal for a few hours is of significantly smaller scale. Lastly, since eggs are part of the totally passive plankton, these results suggest that other passive plankton patches, or gaps, would have been equally coherent and slowly changing with time, and that aggregating organisms would have had to expend relatively little energy in maintaining a patch under these conditions.

DISCUSSION

The unusual circumstances of this set of observations have led to a new appreciation for the origin of small-scale distribution of anchovy eggs and the three-day persistence of this distribution. The scale and intensity of this pattern may have important consequences, both for comparative sampling of the habitats of the eastern boundary currents, and for interpreting predation. Because this set of samples was taken for other purposes, we will discuss the relations between these observations and similar observations, the implications of the persistence of pattern, and what sampling design and effort are necessary to advance the pattern studies to an analytical level.

Sampling Consequences

The high variability of plankton samples has been attributed to variations in towing procedure (Windsor and Walford 1936); heterogeneous water masses (Windsor and Clarke 1940; Cassie 1959); and aggregations of organisms (Ricker 1937; Langford 1938; Barnes and Marshall 1951). In particular, sardine eggs, which last in the plankton only a few days, are known to be aggregated at spawning (Silliman 1946; Taft 1960) and diffuse away from school-sized (tens to hundreds of meters diameter) patches, which persist for several days (Smith 1973). Aggregations of organisms and heterogeneous water masses occur at several scales and may persist over various time periods (Haury et al. 1978), and our perception of the pattern is profoundly influenced by frequency and duration of cruises, the spacing between stations, and the width and trajectory of the sampling instruments as well as the length of tow (Weibe 1972).

Number of samples. The required number of observations can be determined for a first approximation from an existing set (Santander et al. 1982) or from a pilot cruise. In general, pattern is small-scale relative to the distribution of the species, so a pilot study of spawning pattern can be conducted in a small area (100 × 100 km). The results of this study indicate that one must be separated from an area by either space (km) or time (days) to gather a valid replicate versus a redundant sample. The same is true of the pilot study conducted on existing sample results.

If a study requires precise data on a single day's spawning, the variance of the total eggs will be an underestimate of the individual day's spawning by the ratio of the persistence of the egg and the sample variance of the total eggs: for an egg that persists 3

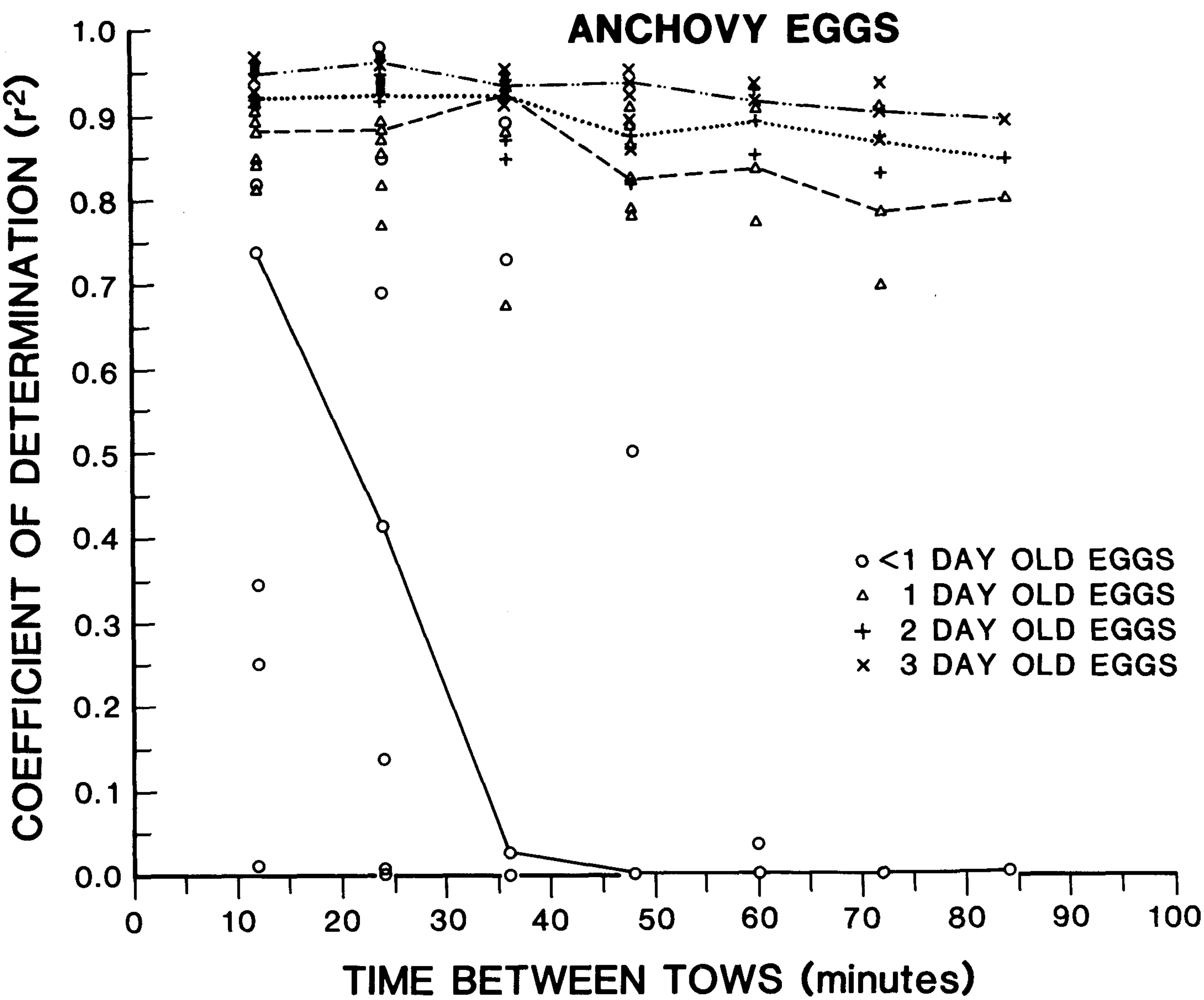

Figure 2. The persistence of correlation between tows as a function of time between tows. Points are from individual values of coefficient of determination for adjacent tows (7 sets), tows separated by 24 minutes (6 sets), tows separated by 36 minutes (5 sets), etc. The lines connect the medians of each interval. (For simplicity, only the nominal interval is graphed: the actual intervals varied from 6 to 36 minutes, with 92% of intervals between 9 and 17 minutes and 51% between 11 and 13 minutes. For complete distribution see Appendix Table 2.)

days, the variance of the total eggs can be multiplied by three to estimate the required number of samples for a given standard error. If the study requires 200 observations to suitably estimate the total number of eggs, it would require 346 samples to estimate the number of eggs spawned in a single day. To describe the onset of spawning between 1800 and 0200 hours with equal precision, it would take a similar number of samples each hour.

Geographic position of samples. Anchovy spawning habitats seem to vary considerably in different eastern boundary currents. The spawning habitat off North America comprises broad regions in relatively permanent gyrals. The spawning habitat off Peru is relatively narrow (Santander et al. 1982; Smith et al. 1983); the spawning habitat off South Africa appears to be a fast-moving coastal jet (Shelton and Hutchings 1982). The current practice is to make 1,000 observations per survey off California (Smith and Hewitt 1984). This may be the minimum required when one considers that the sample must encompass the spawning area, obtain a representative mean, and provide an estimate of egg mortality. Where the spawning habitat is too narrow to provide sufficiently independent adjacent samples, as in Peru, it may be necessary to occupy the habitat more than once. Where the habitat

TABLE 10
Ocean and Atmospheric Predictability Time for Different Scales of Motion

Scale	Predictability time	
	Atmosphere	Ocean
10 m	—	10 min.
100 m	3 min.	1.5 hr
1 km	13 min.	10 hr
10 km	1 hr	3 days
100 km	4 hr	3 weeks
1000 km	1 day	4 months
10000 km	5.5 days	x years

Modified from Platt et al. (1977)

is extremely dynamic, it may be necessary to expand the pattern with time to accommodate the rapidly moving jet and evaluate the survivors.

Consequences for the Study of Pattern

The egg distribution of schooled, coastal, pelagic spawning fish sufficiently resembles coastal plankton blooms like red tide (Kierstad and Slobodkin 1953; Wroblewski 1984) to allow evaluation of the influence of turbulent diffusion and transport at spawning time (Lasker 1975; Bakun and Parrish 1982). The 60 samples reported here (480 observations in samples of 8 per station) are not sufficiently numerous to describe even mortality, so we may expect the number of samples necessary to exceed 200 if interannual variations are relatively large. The assembly of 5 years of egg distribution observations (1,666 positive samples) was adequate to estimate mortality and dispersal (Smith and Hewitt 1984). There was no evidence of offshore transport in the 3-day period for which eggs persist: transport may be inferred from the distribution of older versus younger larvae (Smith 1972 [sardine, Fig. 6; anchovy, Fig. 7]; Hewitt and Methot 1982 [anchovy, Tab. 4, Fig. 15]). Because of this latter phenomenon, higher volumes will have to be filtered over longer distances than used for the vertical tows, to effectively describe transport. Also, the observations must be extended over time to describe transport in the mesoscale.

Predictability in the Eastern Boundary

A new process of modeling, empirical measurements specified by models, and modification of models based on new measurements is beginning (Bakun et al. 1982). For eastern boundary currents the models will have an atmospheric component, an oceanographic component, and a series of biological effects. We must remember that some causative factors in the air and ocean will remain unpredictable over certain space and time scales; thus biological responses will remain unpredictable. The nature of the problem of matching these time and space scales may be seen in Table 10. It seems reasonable to conclude from correlation of replicate samples for eggs less than 8 hours old that the pattern which yielded this result was on the order of hundreds of meters or the space scale of a fish school (perhaps in motion during spawning). Thus there is a new opportunity to design process-oriented cruises with the goal of determining the most important time and space scales of organisms of known age and distributional heterogeneity.

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APPENDIX

TABLE 1
Station Data for Replicate Series

CalCOFI line	CalCOFI station	Date	Time	10-meter temperature
90.0	28.0	790122	2043	14.8
82.0	47.0	790127	0810	13.1
83.0	42.0	790127	1254	13.6
83.0	40.6	790127	1832	13.5
87.0	35.0	790128	0645	13.7
89.6	34.6	790128	1419	14.1
93.0	30.0	790129	1855	13.8
93.0	35.0	790129	2313	14.1
93.0	40.0	790130	0337	14.4
93.0	45.0	790130	0757	13.2
89.5	41.0	790131	0959	13.2
88.4	40.6	790131	1413	13.5
89.2	32.9	790201	0813	13.6
90.1	32.0	790201	1150	13.7
90.8	35.1	790201	1549	14.0
91.7	39.8	790201	2057	13.9
90.6	42.8	790202	0127	14.0
88.9	45.3	790202	0632	12.9
87.6	44.7	790202	1031	13.2
86.3	44.8	790202	1905	13.0
86.1	42.6	790203	0010	13.1
84.3	43.4	790203	1108	13.0
83.8	47.2	790203	1444	13.1
83.9	52.3	790203	1839	13.1
89.4	51.2	790204	0947	13.4
91.9	44.2	790204	1855	13.3
92.9	38.1	790204	2346	13.6
91.9	32.8	790205	0423	13.6
92.2	27.7	790205	0817	13.5
93.5	27.4	790205	1142	14.0
93.8	31.8	790206	1945	14.3
91.9	40.6	790207	0728	13.8
90.8	46.5	790207	1222	13.2
90.5	44.2	790207	2127	13.8
92.2	42.9	790208	0845	14.1
93.1	45.2	790208	1717	13.8
91.8	45.8	790208	2104	13.9
92.7	40.9	790209	0126	13.9
94.9	50.2	790209	1802	13.7
96.7	50.2	790209	2213	14.3
96.0	45.9	790210	0319	14.2
94.4	38.6	790210	1106	13.9
93.3	34.7	790210	1526	14.4
92.8	31.6	790210	1859	13.9
91.2	30.2	790211	0040	12.4
91.9	34.3	790211	0540	14.1
91.2	37.8	790211	0939	14.7
89.7	36.5	790211	1400	14.7
88.9	40.7	790211	1739	13.8
88.2	43.9	790212	1519	14.0
87.8	39.1	790212	1907	13.3
86.4	38.5	790212	2300	13.7
85.6	45.8	790213	0749	13.2
82.5	43.3	790214	0640	13.4
83.8	40.6	790214	1050	13.8
85.2	37.2	790214	1452	13.9
86.5	33.9	790214	1920	13.8
89.4	30.6	790215	0320	13.8
90.2	29.3	790215	0655	14.0
91.7	28.0	790215	1050	14.9

TABLE 2
Distribution of Intervals between Tows

Interval between tows (min)	Proportion of observations	
6	.011	*
8	.017	**
10	.089	*******
12	.511	***********************************
14	.260	******************
16	.060	*****
18	.026	**
20	0	
22	.017	**
24	0	
26	.003	*
28	0	
30	0	
32	.003	*
34	0	
36	0	
38	.003	*

TABLE 3
Program to Estimate Parameters of a Negative Binomial Distribution

Original program by Hewitt Tektronix (1977)
Converted by Smith to TRS-80 (1980)
Converted by Smith to VAX (1982)

```
10  rem uses three methods for estimating k of negative binomial"
20  K=0
30  K1=0
40  K2=0
50  PRINT"Enter total number of observations in sample, number of"
60  PRINT"zero observations, mean and standard deviation of all"
70  PRINT"observations."
80  INPUT N,Z,M,S
85  V=S*S
90  PRINT "trial k = ";
100 INPUT K
110 X=-LOG(Z/N)/K-LOG(1+M/K)
120 PRINT"residual = ";X
130 PRINT "press enter for another trial, otherwise any key"
140 INPUT Q$
150 IF Q$=" " GO TO 90
160 K1=(M*M)/(V-M)
170 PRINT"Enter the observation frequency table: first value"
180 PRINT"then frequency thus 15,6 - - enter 999,0 when finished"
190 DIM I1(1000),R(1000)
200 I=1
210 PRINT I; "value = ";
220 INPUT I1(I)
230 IF I1(I)=999 THEN 290
240 PRINT "frequency = ";
250 INPUT R(I)
260 A=I
270 I=I+1
280 GO TO 210
290 PRINT "trial K = ";
300 INPUT K2
310 B=1
320 U=0
330 FOR J = 1 TO A
340 Q=0
350 FOR I = B TO A
360 Q=R(I)+Q
370 NEXT I
380 V=Q/(K2+J-1)
390 U = U + V
400 B=B+1
410 NEXT J
420 X=N*LOG(1+M/K2)-U
430 PRINT "residual = ";X
440 PRINT "want another iteration?"
450 INPUT Q$
460 IF Q$=" " GO TO 290
470 PRINT "from the proportion of zeroes ........................................................... ";K
480 PRINT "by the method of moments ............................................................... ";K1
490 PRINT "by maximum likelihood .................................................................. ";K2
500 END
```