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The relationship between vertebral number and water temperature in cod

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An inverse relationship between water temperature during early development and mean vertebral number (\overline{VS}) , includes urostyle) is established for cod populations throughout the North Atlantic, but the extent to which differences in \overline{VS} are inherited is unknown. The \overline{VS} of different year classes of cod from the North Sea shows some dependence on water temperature and the year class should therefore be taken into account, where possible, when seeking evidence of separation between stocks. Values of \overline{VS} for populations around the British Isles are plotted on the chart of mean March surface temperature and in general agree with the established temperature— \overline{VS} relationship. Two areas for which the vertebral numbers seem anomalous are the English Channel and the northeast Irish Sea and these anomalies are discussed.

Introduction

Since the classic paper by Schmidt (1930), an enormous amount of work has been carried out to determine the average number of vertebrae (\overline{VS}) in different populations of cod (Gadus morhua L.) throughout the North Atlantic for stock separation studies (see Table 1). Differences in \overline{VS} in fish arise owing to hereditary factors and to the influence of the environment, particularly water temperature, during early life. An inherited difference in VS between Irish Sea and North Sea plaice, reared under identical conditions, was demonstrated by Purdom and Wyatt (1969). The effect of temperature during early life has been described by Tåning (1946) who induced differences in VS of sea trout of up to 1.5 in full brothers and sisters reared under different temperature regimes. Similar work on Fundulus majalis (Walbaum) was reported by Fahy (1972). The relationship between water temperature during early development of haddock and \overline{VS} has been investigated by Clark and Vladykov (1960) using extensive survey data. They concluded that a single temperature- \overline{VS} relationship applies to the species throughout its range. No published relationship of this kind seems to exist for cod in spite of numerous records of \overline{VS} and frequent mention of the influence of temperature. In the present paper a temperature-VS relationship is derived and some suggestions are made about its application to problems of stock identity.

Results

Figure 1 shows the \overline{VS} for cod populations from all parts of the North Atlantic plotted against the surface temperature during their month of spawning. The data sources are given in Table 1. Temperature data are from Stefansson (1962), ICNAF (1968), Hydrographic Office, U.S. Navy Dept. (1944), ICES (1962), Clark and Vladykov (1960) and some of my own. Samples ranging in size from 20 to 4594 fish from a total of 70 locations throughout the North Atlantic are included. In a small number of cases the exact position of the sample and the time of spawning had to be guessed and the average monthly temperature interpolated from contour charts. It seems reasonable to expect that this will increase the error variance in the relationship rather than introducing a bias. The highest values (\overline{VS} of 55 and above) occur off Newfoundland and Labrador, For the latter area Postolaky (1968) reports that the development of eggs and larvae in the surface layer proceeds mainly at 0° C (or less). Lowest \overline{VS} are recorded from Rockall and the Bristol Channel, where average surface temperatures in March are over 8°C. The vertebral count frequencies for most samples are given in the Appendix Table 1.

Table 1. Mean vertebral counts of cod (including urostyle) in the North Atlantic.

Schmidt (1930) 1 66°53′N 20°47′W 120 52·96 0·65 2 66°01′N 17°30′W 287 52·96 0·71 3 65°40′N 14°10′W 370 53·23 0·64 4 65°17′N 13°59′W 1290 52·85 0·69 5 64°35′N 13°15′W 73 53·26 0·71 6 63°44′N 22°57′W 186 52·73 0·71 7 Faroe Plateau 2746 52·28 0·62 Schmidt (1930) 8 63°08′N 7°30′E 79 53·76 0·62 9 68°00′N 14°00′E 148 53·67 0·71 10 69°38′N 33°12′E 66 53·82 0·68 11 70°15′N 19°30′E 76 52·95 0·76 12 70°24′N 32°00′E 81 53·42 0·77 Dannevig (1947) 13 59°33′N 10°27′E 3242 51·94 0·71-0·88 Schmidt (1930) 14 41°18′N 70°02′W 70 52·90 0·68 15 43°59′N 68°08′W 58 53·97 0·88 16 43°36′N 62°18′W 93 54·29 0·80 17 46°00′N 61°35′W 72 53·86 0·92 18 47°35′N 52°54′W 467 53·60 0·74 21 61°00′N 47°00′W 200 53·42 0·69 Mackenzie and 23 Ingonish 2172 53·96 Smith (1955) 24 Canso 915 54·13 25 Quereau 3481 54·22 26 Sable Island 7031 54·04 0·77	4·5 3·0 2·0 0·0 0·8 0·8 0·8 1·5 0·0 0·8
3 65°40′N 14°10′W 370 53·23 0·64 4 65°17′N 13°59′W 1290 52·85 0·69 5 64°35′N 13°15′W 73 53·26 0·71 6 63°44′N 22°57′W 186 52·73 0·71 7 Faroe Plateau 2746 52·28 0·62 Schmidt (1930) 8 63°08′N 7°30′E 79 53·76 0·62 9 68°00′N 14°00′E 148 53·67 0·71 10 69°38′N 33°12′E 66 53·82 0·68 11 70°15′N 19°30′E 76 52·95 0·76 12 70°24′N 32°00′E 81 53·42 0·77 Dannevig (1947) 13 59°33′N 10°27′E 3242 51·94 0·71–0·88 Schmidt (1930) 14 41°18′N 70°02′W 70 52·90 0·68 15 43°59′N 68°08′W 58 53·97 0·88 16 43°36′N 62°18′W 93 54·29 0·80 17 46°00′N 61°35′W 72 53·86 0·92 18 47°35′N 59°10′W 49 54·16 0·85 19 47°34′N 52°42′W 65 54·91 1·07 20 65°23′N 52°54′W 467 53·60 0·74 21 61°00′N 47°00′W 200 53·42 0·69 22 65°40′N 37°10′W 183 53·14 0·67 Mackenzie and 23 Ingonish 2172 53·96 Smith (1955) 24 Canso 915 54·13 25 Quereau 3481 54·22	3·5 3·8 4·0 5·5 6·5 4·5 1·5 3·0 1·5 7·7 4·5 3·0 2·0 0·0 0·8 0·8 0·8 1·5 0·8 0·8
4 65°17′N 13°59′W 1290 52·85 0·69 5 64°35′N 13°15′W 73 53·26 0·71 6 63°44′N 22°57′W 186 52·73 0·71 7 Faroe Plateau 2746 52·28 0·62 Schmidt (1930) 8 63°08′N 7°30′E 79 53·76 0·62 9 68°00′N 14°00′E 148 53·67 0·71 10 69°38′N 33°12′E 66 53·82 0·68 11 70°15′N 19°30′E 76 52·95 0·76 12 70°24′N 32°00′E 81 53·42 0·77 Dannevig (1947) 13 59°33′N 10°27′E 3242 51·94 0·71–0·88 Schmidt (1930) 14 41°18′N 70°02′W 70 52·90 0·68 15 43°59′N 68°08′W 58 53·97 0·88 16 43°36′N 62°18′W 93 54·29 0·80 17 46°00′N 61°35′W 72 53·86 0·92 18 47°35′N 59°10′W 49 54·16 0·85 19 47°34′N 52°42′W 65 54·91 1·07 20 65°23′N 52°54′W 467 53·60 0·74 21 61°00′N 47°00′W 200 53·42 0·69 Mackenzie and 23 Ingonish 2172 53·96 Smith (1955) 24 Canso 915 54·13 25 Quereau 3481 54·22	3·8 4·0 5·5 6·5 4·5 4·5 1·5 3·0 1·5 7·7 4·5 3·0 2·0 0·0 0·0 0·8 0·8 1·5 0·8 1·5 0·8 0·8
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Schmidt (1930) 8 63°04'N 7°30'E 79 53·76 0·62 9 68°00'N 14°00'E 148 53·67 0·71 10 69°38'N 33°12'E 66 53·82 0·68 11 70°15'N 19°30'E 76 52·95 0·76 12 70°24'N 32°00'E 81 53·42 0·77 Dannevig (1947) 13 59°33'N 10°27'E 3242 51·94 0·71-0·88 Schmidt (1930) 14 41°18'N 70°02'W 70 52·90 0·68 15 43°59'N 68°08'W 58 53·97 0·88 16 43°36'N 62°18'W 93 54·29 0·80 17 46°00'N 61°35'W 72 53·86 0·92 18 47°35'N 59°10'W 49 54·16 0·85 19 47°34'N 52°42'W 65 54·91 1·07 20 65°23'N 52°54'W 467 53·60 0·74 21 61°00'N 47°00'W 200 53·42 0·69 Mackenzie and 23 Ingonish 2172 53·96 Smith (1955) 24 Canso 915 54·13 25 Quereau 3481 54·22	5·5 6·5 4·5 4·5 1·5 3·0 1·5 7·7 4·5 3·0 2·0 0·0 0·0 0·8 0·8 0·8 0·8 0·8 0·8
Schmidt (1930) 8 63°08′N 7°30′E 79 53·76 0·62 9 68°00′N 14°00′E 148 53·67 0·71 10 69°38′N 33°12′E 66 53·82 0·68 11 70°15′N 19°30′E 76 52·95 0·76 12 70°24′N 32°00′E 81 53·42 0·77 Dannevig (1947) 13 59°33′N 10°27′E 3242 51·94 0·71–0·88 Schmidt (1930) 14 41°18′N 70°02′W 70 52·90 0·68 15 43°59′N 68°08′W 58 53·97 0·88 16 43°36′N 62°18′W 93 54·29 0·80 17 46°00′N 61°35′W 72 53·86 0·92 18 47°35′N 59°10′W 49 54·16 0·85 19 47°34′N 52°42′W 65 54·91 1·07 20 65°23′N 52°54′W 467 53·60 0·74 21 61°00′N 47°00′W 200 53·42 0·69 22 65°40′N 37°10′W 183 53·14 0·67 Mackenzie and 23 Ingonish 2172 53·96 Smith (1955) 24 Canso 915 54·13 25 Quereau 3481 54·22	6·5 4·5 4·5 1·5 3·0 1·5 7·7 4·5 3·0 2·0 0·0 0·0 0·8 0·8 0·8 0·8 0·8 0·8
Schmidt (1930)	4·5 4·5 1·5 3·0 1·5 7·7 4·5 3·0 2·0 0·0 0·8 0·8 0·8 1·5 0·8 1·5 0·0 0·8 0·8
9 68°00'N 14°00'E 148 53·67 0·71 10 69°38'N 33°12'E 66 53·82 0·68 11 70°15'N 19°30'E 76 52·95 0·76 12 70°24'N 32°00'E 81 53·42 0·77 Dannevig (1947) 13 59°33'N 10°27'E 3242 51·94 0·71–0·88 Schmidt (1930) 14 41°18'N 70°02'W 70 52·90 0·68 15 43°59'N 68°08'W 58 53·97 0·88 16 43°36'N 62°18'W 93 54·29 0·80 17 46°00'N 61°35'W 72 53·86 0·92 18 47°35'N 59°10'W 49 54·16 0·85 19 47°34'N 52°42'W 65 54·91 1·07 20 65°23'N 52°54'W 467 53·60 0·74 21 61°00'N 47°00'W 200 53·42 0·69 22 65°40'N 37°10'W 183 53·14 0·67 Mackenzie and 23 Ingonish 2172 53·96 Smith (1955) 24 Canso 915 54·13 25 Quereau 3481 54·22	4·5 1·5 3·0 1·5 7·7 4·5 3·0 2·0 0·0 0·8 0·8 0·8 1·5 0·0 0·8
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Smith (1955) 24 Canso 915 54·13 25 Quereau 3481 54·22	0·8 0·6 1·8
25 Quereau 3481 54·22	0·6 1·8
· · · · · · · · · · · · · · · · · · ·	1.8
20 Savie Island 7031 34:04 7077	and the second s
27 St. Margaret 2863 53.86	1.1
28 Browns 4388 53·80	2.4
29 Digby 1730 53·51 J	2.8
Thompson (1943) 30 Banquereau 82 53-99 0-65	0.6
31 44°30′N 51°00′W 60 53·38 0·95	4.5
32 48°40′N 53°00′W 99 55·43 0·87	0.8
33 52°00′N 53°30′W 90 55·20 1·01 34 53°00′N 55°00′W 60 55·17 0·81	0·2 -1·0
35 53°30′N 55°00′W 91 55.07 0.97	-1·0 -1·0
36 54°30′N 57°00′W 29 54·86 0·86	-1.0
Stanek (1968) 37 52°30′N 52°00′W - 55·26 -	0.0
38 51°20′N 51°30′W - 55·34 -	-0.5
39 50°30′N 52°30′W – 54·83 –	0.0
Schmidt (1930) 40 60°52′N 8°12′W 120 51·77 0·64	8.0
41 57°00′N 14°00′W 91 51·47 0·62	8.7
42 53°24′N 3°58′W 193 51·69 0·64	7.0
43 55°25′N 5°30′W 75 51.67 0.62	7.0
44 58°14′N 6°18′W 272 51·87 0·55	7.5
45 58°59′N 2°53′W 200 51·91 0·61	6.8
46 56°01′N 3°22′W 84 52·24 0·61	5·5 5·8
47 54°46′N 0°28′E 165 52·04 0·64 48 53°03′N 2°07′E 94 52·09 0·74	5·8 5·3
48 53°03′N 2°07′E 94 52·09 0·74 49 53°00′N 4°45′E 97 52·19 0·63	5·3
50 54°12′N 7°53′E 205 52·30 0·63	4·0
50 54 12 14 7 53 E 265 52 56 0 65 51 56°39'N 7°58'E 150 52.06 0.65	4.3
52 55°28′N 7°55′E 200 52·28 0·55	4.0
53 60°23′N 5°20′E 197 52·43 0·67	4.0
54 59°24'N 5°17'E 93 52·44 0·74 Unpublished data from	4.0
	5.5
Seals Research 55 Flamborough 465 52·23 0·70 Division of the 56 Gt. Fisher 600 52·30 0·72	5.5
Institute of 57 Dogger 531 52.44 0.70	5·3 5·2
Marine 58 S North Sea 531 52-30 0-67	6.0
Environmental 59 off Hastings 20 52-25 0-64	7.5
Research (Plymouth) 60 off Brixham 48 52·13 0·84	$9.\overline{2}$
61 S Irish Sea 473 51.72 0.68	8.0

Cont'd

Table 1 cont'd.

Source	Sam- ple No.	Area of sampling	No. of fish	Mean No. of vertebrae	Standard deviation	Temperature at spawning (°C)
	62	NE Irish Sea	147	51.56	0.70	6.0
Lefranc (1970) Present study	63	North Channel	283	51.72	0.78	7-2
	64	West of Scotland	535	51.70	0.69	8.3
	65	off Southend	36	52-47	0.61	6.0
	66	E Channel	488	52.33	_	7-5
	67	Bristol Channel	209	51.58	0.72	8.3
	68	County Down	469	51.80	0.69	7⋅0
	69	NE Irish Sea	368	51.60	0.87	6.0
	70	S Irish Sea	52	51.67	0.65	7.5

The equation for the regression line plotted in Figure 1 is:

 \overline{VS} (including urostyle) = $54.45 - 0.361 \times T$ (°C)

The correlation coefficient (r) is -0.906 for 68 degrees of freedom (probability of r > 0.302 is 0.01 for 70 d.f.). The regression accounts for 82% of the variance in vertebral count and an increase in water temperature of 1°C would be expected to give a decrease of 0.361 in \overline{VS} .

Clark and Vladykov (1960) fitted a curve to their data, but in the present case square root and log-

arithmic transformations of the vertebral count gave only very small improvements in r. The curves produced by the transformations cannot be plotted on Figure 1 because they are indistinguishable from the straight line.

Statistically significant differences in \overline{VS} between two or more populations are therefore likely to be detected when the difference in temperature at and after spawning between the two areas and also the sample size are sufficiently large. Differences in \overline{VS} would be expected between year classes from the same area as well as in samples from different areas,

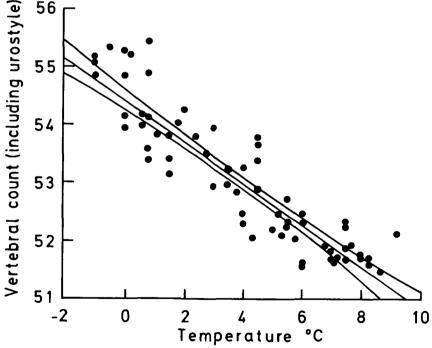


Figure 1. Relationship between temperature in the month of spawning and \overline{VS} for cod in all parts of the North Atlantic.

if the year-to-year fluctuations in temperature are sufficiently large. Table 2 shows values for five year classes of North Sea cod sampled at North Shields, Grimsby and Lowestoft. In Figure 2, which is to the same scale as Figure 1, these are plotted against March surface temperature averaged over the area sampled (data in Table 2). The regression line from Figure 1 is also shown. The \overline{VS} of the 1963 year class (Table 2) is higher than that of the other year classes, but lower than might be expected from the regression line. One explanation to this slight discrepancy is that the regression includes any inherited differences in VS between stocks which may exist, whereas the differences between North Sea year classes are due to environmental causes. It may be that differences in VS between stocks, which arose originally as a result of differences in water temperature acting on

Table 2. \overline{VS} of North Sea cod sampled at North Shields, Grimsby and Lowestoft and mean March surface temperature averaged over the area of sampling.

Year class	T(°C)	V S	No. of fish		
1963	3.3	52.56	185		
1964	5·1	52.27	171		
1965	5-1	52.39	409		
1966	5.7	52.26	922		
1967	6.4	52.07	351		

the same genotype, have gradually become genetically fixed. Nevertheless, in comparing \overline{VS} for samples from different areas it is advisable to take account of the year-class composition of the sample and the annual temperature regime. But even without such detailed information it may still be possible to draw broad conclusions from aggregated data and to detect anomalies in relation to mean surface temperature and the values derived from the regression.

An example of the aggregated approach is shown in Figure 3 in which data from around the British Isles are plotted on the mean March surface temperature chart (from ICES, 1962). From the regression one would expect \overline{VS} above 52 at water temperatures below 6.8°C. Except for one sample from Orkney, where March surface temperatures are high, all the North Sea values are above 52. In the English Channel the values are also above 52, but the temperature over most of the area is above 7°C. The Eastern Channel is a transition area in which the average March surface temperature drops from over 8°C to less than 6.5°C within a short distance and for which it is therefore difficult to specify a temperature at spawning without detailed information on the fine scale distribution. In comparing his values of \overline{VS} from the Strait of Dover with those of other areas Lefranc (1970) did not include the urostyle, whereas Schmidt (1930) and Dannevig (1947) did. His conclusion, that the fish which he sampled were spawned locally, may be correct, but

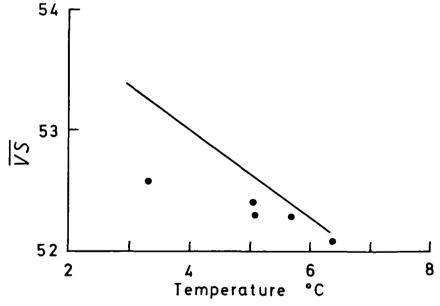


Figure 2. VS for the 1963 to 1967 year classes from the North Sea.

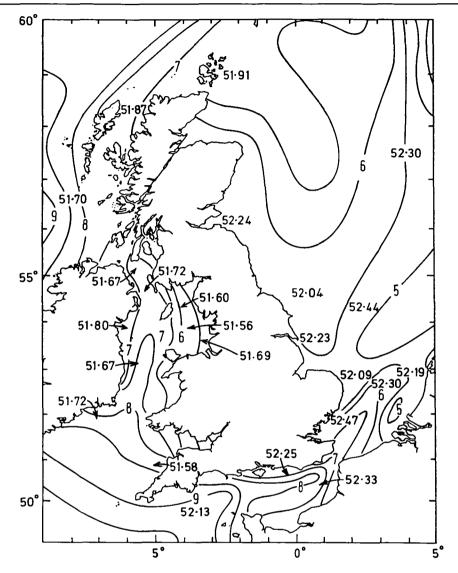


Figure 3. \overline{VS} for areas around the British Isles, plotted on the mean March surface temperature chart (from ICES, 1962).

his reasoning, that this is demonstrated by the "low" vertebral count owing to the relatively warm water in the Strait of Dover, is not. Similarly the other cod sampled in the English Channel may have originated from the relatively cold parts of the Eastern Channel or from the North Sea.

All the samples from the areas west of the British Isles show \overline{VS} below 52, in line with the generally warmer water temperatures. In the northeast Irish Sea, however, the surface temperature falls to 6°C and below in March, so that one would expect the

 \overline{VS} to be above 52. Instead sampling over a long period has consistently given values as low as 51.56. These low values may be due to consistent large scale migration into the area from warmer waters to the south and tagging experiments are being carried out to test this hypothesis. A positive result would still leave the problem of explaining the fate of the eggs which are spawned in the northeast Irish Sea. The possibility that the lower \overline{VS} is an inherited character can also not be excluded.

Appendix

Appendix Table 1. Vertebral count frequencies for cod samples (sample numbers are the same as those of Table 1).

Sample No.	48	49	50	51	No. 8	SF verteb	54	55	56	57	58	No. of fish	
1	_	_	_		28	69	23		-	_	~	120	
2	-	-	_	4	63	163	54	3	_	-	~	287	
3	-	-	-	2	36	210	118	4	-	-	~	370	
4	_	_	-	28	345	715	193	9	-	_	~	1 290 73	
5 6	_	_	_	- 4	10 66	35 92	27 24	1	-	_	~	186	
7	_	_	_	196	1625	881	42	2	_	_	~	2746	
8 9	_	_	_	_	1	24	47 75	7 15	_	_	~	79 148	
10	_	_	_	_	6	52 22	73 34	10	_	_	~	66	
11	_	_	_	2	18	38	18	-	_	_	~	76	
12	_	_	_	_	9	34	33	5	_	_	_	81	
13	1	4	93	725	1729	654	35	1	_	_	_	3242	
									_	-			
14	-	-	-	-	19	40	10	1	_	-	~	70	
15		-	_	-	4	11	26	17	5	_	~	58 93	
16 17	-	-	_	-	-	15	41	32	2	-	-	72	
18	_	_	_	1	3	19 11	33 22	14 13	3	_	~	49	
19	_	_	_	_	_	6	17	24	13	5	~	65	
20	_	_	_	_	27	179	219	40	2	_	_	467	
21	_	_	_	_	16	92	85	7	_	•	-	200	
22	_	_	_	2	28	96	57	_	_	_	~	183	
30	_	_	_	_	1	14	53	13	1	_	_	82	
31	_	_	_	2	7	24	20	7	_	_	_	60	
32	_	_	_	_	_	-	13	41	35	9	1	99	
33	_	_	_	_	_	5	16	32	31	5	i	90	
34	_	_	_		_	_	11	26	20	3	-	60	
35	_	-	_	_	_	3	25	32	25	6	_	91	
36	_	_	_	_	_	2	7	13	7	_	_	29	
40	_	_	_	40	70	8	2	_	_	_	_	120	
41	_	_	3	45	40	3	_	_	_	_	_	91	
42	_	_	5	62	114	11	1	_	_	_	_	193	
43	_	_	2	25	44	4	_	_	_	_	-	75	
44	_	_	_	61	185	26	_	_	_	_	_	272	
45	_	_	1	44	127	28	_	_	_	_	_	200	
46	_		1	5	51	27	_	_	-	_	_	84	
47	-	-	-	31	97	37	_	-	-	_	_	165	
48	_	-	1	16	54	20	3	_	_	-	-	94	
49	-	-	1	9	58	29	-	-	-	-	_	97	
50	-	-	1	12	121	67	4	_	-	-	-	205	
51	_	-	1	24	90	35	-	_	-	-	_	150	
52	_	-	-	9	127	63	1	-	-	-	-	200	
53	-	-	-	13	94	83	7	_	-	_	-	197	
54	-	-		7	45	34	7	_	-	_	-	93	
55	_	-	4	55	241	160	5	-	-	-	-	465	
56	-	-	1	70	297	213	19	_	_	-	_	600	
57	_	-	3	35	241	232	20	_	_	_	-	531	
58	_	_	3	50	270	202	6		-	-	-	531	
59 60	-	_	-	2	11	7	-	_	_	-	-	20 38	
61	-	-	1	7 152	17 261	12 45	1 1	-	_	-	-	473	
62	_	_	14 7	61	68	11	1	_	_	_	_	147	
63	_	_	12	98	135	34	4	_	_	_	_	283	
64	_	_	20	173	293	48	1	_	_	_	_	535	
65	_	_	-	2	15	19	_	_	_	_	_	36	
	-						_		-	_		209	
67	_	1	8 9	87	95 266	18	-	-	-	_	-	209 469	
~0		-	9	133	266	60	1	_	_	_	-	サリブ	
68 69		2	29	140	143	51	3	_			_	368	

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