

2. Morphologic Variation of *Nautilus pompilius* from the Philippines and Fiji Islands

by

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Abstract

Morphologic variation of *Nautilus pompilius* Linnaeus (Mollusca, Cephalopoda) is described using the two samples from the Tañon Strait, the Philippines and from the water near the Viti Levu Island, Fiji Islands. In both samples, mature specimens show a distinct sexual dimorphism for the dimensions of many characters, but the parameters representing the form ratio are not different between the sexes. The size difference between the mature specimens from the Tañon and Fiji areas is much larger than that between the sexes in the single sample. Namely, mature animals from the former are generally heavier and larger than those from the latter. This fact suggests a fairly wide geographic variation in this species.

Introduction

The chambered *Nautilus* is the sole living representative of the Ectocochliate Cephalopoda, which had been flourished mainly in the Paleozoic and Mesozoic. Because of the fundamental similarities in shell morphology to many extinct forms (e. g. fossil nautiloids and ammonoids), species of modern *Nautilus* have long attracted the attention of many paleontologists for the biological nature. Indeed, most of previous paleontological works on the extinct shelled cephalopods were based in part upon the comparison with modern *Nautilus*.

However, the deep and geographically isolated habitats of *Nautilus* in the Southwest Pacific cause difficulties in studying the ecology of a natural population. Only several field works have recently been made on *N. pompilius* or *N. cf. pompilius* in the Philippines (HAVEN 1972, 1977), Fiji (WARD et al. 1977; WARD and MARTIN 1980) and Palau (SAUNDERS and SPINOSA 1978) Islands, and on *N. macromphalus* in New Caledonia (WARD and MARTIN 1980).

As a result of these works, such aspects as the vertical distribution, functional morphology and reproductive biology have become made clear. Nevertheless, the genetic

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and phenotypic variation of a population or taxonomic relationships of the *Nautilus* species have little studied.

In the previous report (HAYASAKA et al. 1982), we summarized the preliminary observation on some specimens of *N. pompilius* trapped from the Tañon Strait, the Philippines, together with the detailed habitat conditions and associate fauna in the strait.

On the other hand, HAYASAKA and SHINOMIYA (1982) made the field ecological study around the Fiji Islands in 1982, and collected some specimens of *N. pompilius* on that occasion.

Based on the specimens mentioned above, the relative growth and variation of some morphologic characters in this species have been examined in this paper.

Materials and Methods

This paper is based upon the two samples of *N. pompilius* from the Tañon and Fiji areas. The Tañon sample is composed of 32 specimens, which were captured at several points (120-170 m depth), about 2-3 km off Bindoy, the western side of the Tañon Strait during September 7 to 19th, 1981 by a team of Japanese and Philippine scientists and/or Mr. W. VALOCES and his family (Fig. 1B). Details of the catch records were listed in HAYASAKA et al. (1982, table 10), but we mistakenly identified the sexes of the specimens, B-3, 5, 23-24, 26, and 28-29 in that table.

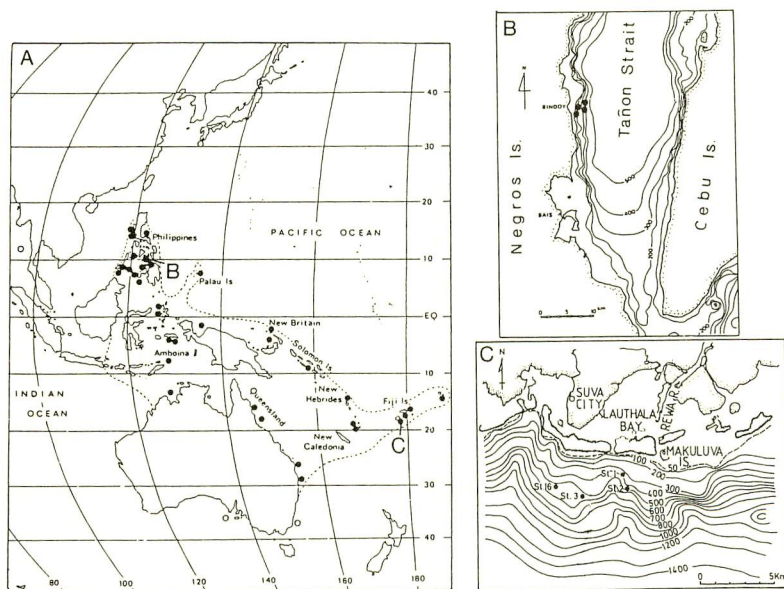


Fig. 1. Index map showing the sampling locations of *N. pompilius* studied. A. Map showing the geographic distribution of *N. pompilius* (adapted from HAMADA 1977). B and C. Sampling points and submarine topography in the Tañon (B) and Fiji (C) areas. The numbers in the topographic maps mean depths in meter.

The Fiji sample consists of 31 specimens, which were trapped at four points (366–549 m depth) about 5 km south from the coast of Suva City, Viti Levu Island during January 3 to 4th, 1982 by HAYASAKA and SHINOMIYA (HAYASAKA and SHINOMIYA 1982; Fig. 1C).

As shown in Fig. 1A, the above two samples of *N. pompilius* were collected from the western and eastern margins of the wide habitat realm of this species.

For morphologic analysis the following continuous characters were measured or weighed by means of a slide caliper of accuracy, 0.05 mm and an automatic balance of accuracy, 0.01 g (abbreviations used in the figures and tables are shown in parentheses); maximum shell diameter (D), maximum whorl breadth (B), maximum whorl height (H), maximum whorl length of colorless shell portion (WL), maximum body length without a siphuncular cord (BL), maximum tentacle sheath length (TL), maximum eye diameter (ED), empty shell weight (SW), and soft tissue weight at a time of capture (BW). Based on these measurements, the four parameters concerning the form ratio, i. e. B/D, H/D, B/H, and D/BL, were also calculated for each specimen.

The sexes of the specimens utilized were determined by the presence of some reproductive organs (for details see HAYASAKA *et al.* 1982), and no sexless immature animal was found in our materials. Specimens with a blacked and thickened shell aperture were treated as full-grown or almost full-grown matures.

Biometric examinations were performed with an aid of a personal computer (NEC, PC-8801), and the following abbreviations were used in the statistics; N: number of specimens in a sample, \bar{X} : arithmetic mean, s: standard deviation, V: coefficient of variability ($=100s/\bar{X}$), r: correlation coefficient, P: probability level.

Morphologic Analysis

A. Sexual dimorphism

The measurements and parameters calculated for the Tañon and Fiji samples are summarized in Tables 1–2 respectively. As shown in these tables, the Tañon sample is composed of mature or almost mature specimens only, while the Fiji one consists of 26 immature (84% to the total) and 5 mature (16%) specimens. Therefore, the statistical test for the sexual difference could only be examined in the former sample. With respect to this problem, we have already demonstrated a distinct sexual difference for the total live weight and shell size in the 52 specimens from the same area (HAYASAKA *et al.* 1982), but the data are insufficient in the mistake for the sex determination of several specimens. Reexamination of the selected 9 characters reveals more concrete data for the sexual dimorphism in *N. pompilius* from the Tañon area (Table 3). As shown in this table, statistically significant difference is present for all examined characters between the mature males and females. Judging from the results of this work and HAYASAKA *et al.* (1982), in the population of the Tañon Strait mature males are regarded to be generally larger and heavier than mature females for the observed morphologic characters. The similar evidence has already been confirmed in the samples of population of the same species from Balanche Bay (New Britain) (WILLEY 1902), Fiji (WARD *et al.* 1977; WARD and MARTIN 1980), of *N. cf. pompilius* or *N. belauensis* from Palau (SAUNDERS and SPINOSA 1978; SAUNDERS 1981), and in the sample of

N. macromphalus from New Caledonia (WARD and MARTIN 1980).

Subsequently, the principal component analysis was made for the four parameters (B/D, H/D, B/H, and D/BL) in the 31 mature or almost mature specimens from the Tañon area. The purpose of this analysis is to determine whether or not the sexual dimorphism is also expressed in the basic form ratio. The results of this analysis and the plots of the first three principal component scores are shown in Table 4 and Fig. 2 respectively. As expressed in Fig. 2, the mature males and females are closely related morphologically for variables X_1 , X_2 , and X_3 , and no significant sexual difference is expressed for the basic body proportion. It should be noted that the first three principal components count for almost 100% of the total variation (Table 4).

B. Average relative growth

As the Fiji sample is composed of variously sized specimens, the average relative growth was examined between a pair of selected morphologic variables using a least square method (regression Y on X) (IMBRIE 1956). The results are illustrated in Fig. 3. The correlation coefficients between a pair of shell diameter (D), whorl height (H)

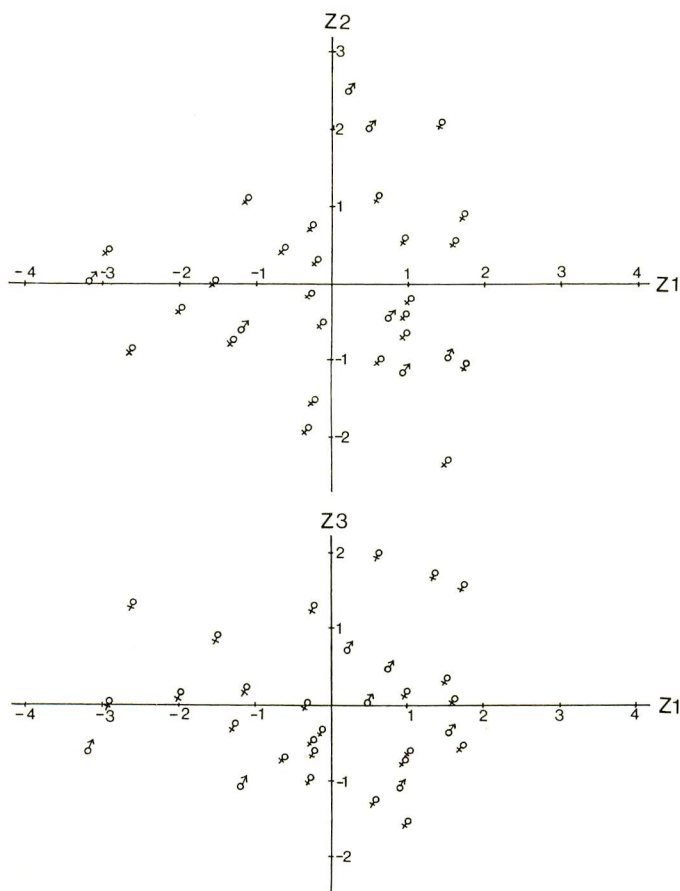


Fig. 2. Plot of the first three principal component scores for the four parameters of form ratio in the mature specimens from the Tañon area.

Table 1. Measurements and basic parameters of the specimens of *N. pompilius* from the Tañon area, the Philippines. The specimens with an asterisk indicate matures.

Specimen	Sex	D _{mm}	B _{mm}	H _{mm}	WL _{mm}	BL _{mm}	TL _{mm}	ED _{mm}	SW _{gr.}	BW _{gr.}	B/D	H/D	B/H	D/BL
*B-1	female	158.3	76.5	94.0	177	146.2	41.0	21.3	158	497	.483	.594	.814	1.083
*B-2	female	151.9	74.4	88.0	144	134.1	39.1	26.1	140	410	.490	.579	.845	1.133
*B-3	female	160.6	78.6	93.9	169	150.2	53.4	26.8	155	545	.490	.585	.837	1.069
*B-4	female	159.1	82.2	93.5	179	139.4	50.2	28.8	154	536	.516	.588	.879	1.141
*B-5	male	180.4	88.3	107.1	205	155.1	69.3	31.8	210	670	.489	.594	.824	1.163
*B-6	female	160.6	79.4	95.2	170	124.7	50.4	26.6	162	528	.494	.593	.834	1.288
*B-7	female	161.3	78.0	95.6	172	144.5	48.0	30.4	155	535	.484	.593	.816	1.294
*B-8	female	161.9	77.0	93.8	147	132.1	45.2	25.3	198	467	.476	.579	.821	1.226
*B-9	female	158.4	76.5	94.9	181	160.5	50.2	27.1	174	541	.483	.599	.806	0.987
*B-10	male	169.5	84.5	104.0	205	160.4	60.1	28.8	186	674	.498	.614	.813	1.057
*B-11	female	157.2	76.8	94.8	187	159.6	52.1	29.2	155	480	.489	.603	.810	0.985
B-12	female	166.2	82.7	99.2	197	164.5	53.0	29.7	185	625	.498	.597	.834	1.010
*B-13	female	165.2	81.8	98.6	174	158.5	51.4	26.0	217	528	.495	.597	.830	1.042
*B-14	female	162.8	80.3	96.3	194	160.6	51.1	26.0	154	591	.492	.592	.831	1.014
*B-15	female	161.9	78.1	95.8	164	150.5	44.5	27.4	154	586	.483	.592	.815	1.076
*B-16	female	173.2	83.5	104.7	185	160.4	50.0	30.4	178	657	.482	.605	.798	1.080
*B-17	female	159.2	79.7	93.4	181	150.6	55.6	28.3	155	620	.500	.587	.853	1.057
*B-18	female	159.9	81.2	96.6	172	152.6	41.3	28.9	150	565	.508	.604	.841	1.048
*B-19	female	158.8	76.9	95.7	176	140.4	48.1	29.1	152	538	.484	.603	.804	1.131
*B-20	female	157.2	81.4	93.6	156	157.3	52.3	28.4	160	530	.518	.595	.870	0.999
*B-21	male	181.2	89.0	108.8	207	—	—	—	216	874	.491	.600	.818	—
*B-22	female	159.1	81.1	94.9	155	142.6	58.5	28.3	147	543	.510	.596	.855	1.116
*B-23	female	174.0	87.8	105.3	218	149.3	44.6	26.3	191	644	.505	.605	.834	1.165
*B-24	male	157.7	78.3	92.4	165	159.4	48.1	31.3	162	513	.497	.586	.847	0.990
*B-25	male	179.4	85.7	105.7	220	157.7	57.4	32.3	201	699	.478	.589	.811	1.138
*B-26	male	170.0	82.0	100.8	200	164.1	57.9	31.2	182	608	.482	.593	.813	1.036
*B-27	male	178.3	90.0	110.3	203	164.1	64.7	33.0	215	820	.505	.619	.816	1.087
*B-28	female	176.7	88.2	109.6	205	146.3	51.5	29.0	194	761	.499	.620	.805	1.208
*B-29	male	164.8	85.0	97.2	192	172.9	68.5	31.2	174	506	.516	.590	.874	0.953
*B-30	female	161.1	79.7	95.3	145	142.5	45.1	25.4	152	573	.495	.592	.836	1.131
*B-31	female	159.5	77.4	94.4	195	138.3	50.0	26.6	165	540	.485	.592	.820	1.153
*B-32	female	161.2	82.4	96.0	187	155.2	55.0	29.2	167	623	.511	.596	.858	1.039

and breadth (B) are lower than that between soft tissue weight (BW) and shell weight (SW), but this owes much to the intervals of the data. The slopes between a pair of D, H, and B indicate almost isometric relationships, while the growth of BW versus SW shows a strong positive allometry. The latter evidence suggests a gradual decrease of buoyancy with growth; but if we demonstrate this hypothesis accurately, the ontogenetic changes in the cameral liquid volume should also be considered.

C. Morphologic comparison between the Tañon and Fiji samples

As already noted, the Tañon and Fiji areas are situated in the opposite marginal areas of the extensive habitat realm of *N. pompilius* (Fig. 1A). Therefore, the two samples examined may be suitable for estimating the geographic variation of this species at morphological level. Table 4 summarizes the statistical data for the selected characters of the mature specimens. As indicated in this table, the mature specimens from

Table 2. Measurements and basic parameters of the specimens of *N. pompilius* from the Fiji area. The specimens with an asterisk indicate matures.

Specimen	Sex	D _{mm}	B _{mm}	H _{mm}	WT _{mm}	BL _{mm}	TI _{mm}	ED _{mm}	SW _{gr.}	BW _{gr.}	B/D	H/D	B/H	D/BL
F-1	male	140.3	74.7	80.4	133	133.2	49.0	22.7	123	252	.532	.573	.929	1.053
F-2	male	145.3	72.4	88.3	156	132.7	52.0	22.9	131	307	.498	.608	.820	1.095
F-3	male	133.7	73.0	77.3	93	129.4	46.3	21.9	116	232	.546	.578	.944	1.033
F-4	female	137.0	69.6	77.9	132	140.0	44.0	21.2	118	271	.508	.569	.894	0.979
F-5	female	102.6	55.6	61.8	25	96.9	34.3	16.4	61	100	.542	.602	.900	1.059
F-6	male	126.6	74.8	87.6	126	139.9	54.0	25.8	126	346	.591	.652	.854	0.905
F-7	male	137.2	71.6	80.4	134	155.7	48.8	22.1	132	285	.522	.586	.891	0.881
F-8	male	146.8	73.1	86.4	152	139.3	51.9	23.0	139	384	.498	.589	.846	1.054
F-9	male	145.6	73.3	87.5	144	141.0	50.1	22.8	128	326	.503	.601	.838	1.033
*F-10	female	137.2	65.1	80.0	137	145.8	44.2	18.8	114	253	.475	.583	.814	0.941
F-11	female	102.6	53.3	59.7	20	82.5	33.0	15.5	55	85	.520	.582	.893	1.244
F-12	female	119.2	64.0	69.2	92	99.5	42.1	20.9	96	156	.537	.581	.925	1.198
*F-13	male	145.0	70.9	86.3	156	153.0	65.6	22.9	123	363	.489	.595	.822	0.948
F-14	male	141.1	74.9	86.0	138	138.0	53.0	23.1	131	300	.531	.609	.871	1.022
F-15	male	148.8	76.2	90.5	156	141.7	55.0	24.2	139	372	.512	.608	.842	1.050
F-16	male	138.0	73.5	86.2	140	126.9	47.9	20.3	127	346	.533	.625	.853	0.920
F-17	male	159.8	75.4	87.4	140	129.1	54.0	23.0	142	330	.472	.547	.863	1.238
F-18	female	123.8	65.4	73.4	103	131.9	44.1	20.0	96	230	.528	.593	.891	0.939
F-19	female	138.5	67.5	78.7	155	135.7	48.0	21.0	136	272	.487	.568	.858	1.021
*F-20	male	134.9	65.6	79.1	158	135.5	46.6	19.8	103	260	.486	.586	.829	0.996
*F-21	male	151.9	75.2	89.0	161	137.5	50.0	22.0	137	407	.495	.586	.845	1.105
F-22	male	140.5	71.8	83.9	154	133.0	44.8	20.9	113	323	.511	.597	.856	1.056
F-23	male	135.9	69.8	81.0	128	119.9	39.1	20.5	100	205	.514	.596	.862	1.133
F-24	male	143.3	73.8	85.8	146	133.1	45.0	21.9	112	314	.515	.599	.860	1.077
*F-25	male	143.7	71.2	85.6	142	127.0	43.6	21.3	125	221	.495	.596	.832	1.131
F-26	female	125.3	67.4	74.0	100	111.2	37.0	18.8	104	166	.538	.591	.911	1.127
F-27	male	119.5	62.7	70.1	68	104.0	35.2	18.0	86	158	.525	.587	.894	1.149
F-28	male	143.5	70.2	85.2	142	123.6	43.1	20.0	120	260	.489	.594	.824	1.161
F-29	male	125.9	67.1	88.3	138	127.6	43.1	21.9	119	291	.533	.701	.760	0.987
F-30	male	144.7	72.8	86.1	181	128.8	43.9	21.1	119	275	.503	.595	.846	1.123
F-31	male	132.5	72.4	78.4	116	103.6	39.0	20.2	99	201	.546	.592	.923	1.279

the Tañon area are mostly larger and heavier than those from Fiji, and furthermore, the difference is much larger than the sexual dimorphism within the single sample. This fact is clearly expressed by the graph showing the disappearance of color bands in the mature stage (Fig. 4). The observed ranges of the examined characters in the two mature samples are, however, not completely separated from each other.

Subsequently, the four parameters concerning the form ratio are compared between the Tañon and Fiji samples using the principal component analytical technique. As the correlation coefficients between each of these parameters and each of other dimensional variables are generally low and in most cases they are not significant at $P=0.01$ (Table 6), these four parameters are regarded to be little influenced by the growth stage or sexes. For this reason, both immature and mature specimens are used for the

Table 3. Statistical data of the selected characters for the mature or almost mature specimens of *N. pompilius* from the Tañon area. For abbreviations see explanations in the text.

[Tañon sample]

Characters	Male specimens N=7	Female specimens N=24
D	$\bar{X}=171.40\text{mm}$, $s=8.46\text{mm}$, $V=4.94$	$\bar{X}=161.89\text{mm}$, $s=5.67\text{mm}$, $V=3.50$
B	$\bar{X}=84.83\text{mm}$, $s=3.88\text{mm}$, $V=4.57$	$\bar{X}=80.08\text{mm}$, $s=3.41\text{mm}$, $V=4.26$
H	$\bar{X}=102.50\text{mm}$, $s=6.16\text{mm}$, $V=6.01$	$\bar{X}=96.37\text{mm}$, $s=4.48\text{mm}$, $V=4.65$
WL	$\bar{X}=198.60\text{mm}$, $s=17.00\text{mm}$, $V=8.56$	$\bar{X}=176.25\text{mm}$, $s=18.70\text{mm}$, $V=10.61$
BL	$\bar{X}=162.00\text{mm}$, $s=5.82\text{mm}$, $V=3.59$	$\bar{X}=148.37\text{mm}$, $s=10.33\text{mm}$, $V=6.96$
ED	$\bar{X}=31.40\text{mm}$, $s=1.31\text{mm}$, $V=4.17$	$\bar{X}=27.53\text{mm}$, $s=2.04\text{mm}$, $V=7.41$
TL	$\bar{X}=60.86\text{mm}$, $s=7.40\text{mm}$, $V=12.16$	$\bar{X}=49.23\text{mm}$, $s=4.85\text{mm}$, $V=4.85$
SW	$\bar{X}=190.00\text{g}$, $s=19.43\text{g}$, $V=10.23$	$\bar{X}=165.50\text{g}$, $s=19.01\text{g}$, $V=11.49$
BW	$\bar{X}=652.90\text{g}$, $s=97.33\text{g}$, $V=14.91$	$\bar{X}=560.96\text{g}$, $s=71.60\text{g}$, $V=12.76$

F- and t- tests for the sexual dimorphism of each character

D	$F=2.23 < 2.42 = F_{0.05}(\lambda=7, 24)$, $P > 0.05$, not significant $t=3.49 > 2.05 = t_{0.05}(\lambda=29)$, $P < 0.05$, significant
B	$F=1.29 < 2.42$, not significant ($P > 0.05$) $t=3.15 > 2.05$, significant ($P < 0.05$)
H	$F=1.89 < 2.42$, not significant ($P > 0.05$) $t=2.93 > 2.05$, significant ($P < 0.05$)
WL	$F=1.21 < 3.44 = F_{0.05}(\lambda=24, 7)$, $P > 0.05$, not significant $t=2.83 > 2.05$, significant ($P < 0.05$)
BL	$F=3.15 < 3.44$, not significant ($P > 0.05$) $t=3.31 > 2.05$, significant ($P < 0.05$)
ED	$F=2.43 < 3.44$, not significant ($P > 0.05$) $t=4.71 > 2.05$, significant ($P < 0.05$)
TL	$F=2.33 < 2.42$, not significant ($P > 0.05$) $t=4.94 > 2.05$, significant ($P < 0.05$)
SW	$F=1.04 < 2.42$, not significant ($P > 0.05$) $t=2.99 > 2.05$, significant ($P < 0.05$)
BW	$F=1.85 < 2.42$, not significant ($P > 0.05$) $t=2.76 > 2.05$, significant ($P < 0.05$)

principal component analysis. The results are summarized in Table 5 and Fig. 5. It is interesting in that the Tañon and Fiji samples are not classified into two groups on the basis of these four parameters. It is, therefore, concluded that the geographic variation of *N. pompilius* between the Tañon and Fiji areas is not expressed by the difference in the form ratio but those in the dimensional characters in the mature

Table 4. Statistical data of the selected characters for the mature or almost mature specimens of *N. pompilius* from the Tañon and Fiji areas. For abbreviations see explanations in the text.

	[Tañon sample]	[Fiji sample]
	N = 31	N = 5
D	$\bar{X}=164.05\text{mm}$, $s=7.45\text{mm}$, $V=7.45$	$\bar{X}=142.54\text{mm}$, $s=6.74\text{mm}$, $V=4.73$
B	$\bar{X}= 81.14\text{mm}$, $s=4.00\text{mm}$, $V=4.93$	$\bar{X}= 69.60\text{mm}$, $s=4.24\text{mm}$, $V=6.09$
H	$\bar{X}= 97.76\text{mm}$, $s=5.46\text{mm}$, $V=5.59$	$\bar{X}= 84.00\text{mm}$, $s=4.27\text{mm}$, $V=5.08$
WL	$\bar{X}=181.29\text{mm}$, $s=20.39\text{mm}$, $V=11.25$	$\bar{X}=150.80\text{mm}$, $s=10.62\text{mm}$, $V=7.04$
BL	$\bar{X}=151.44\text{mm}$, $s=11.04\text{mm}$, $V=7.29$	$\bar{X}=139.76\text{mm}$, $s=9.97\text{mm}$, $V=7.13$
ED	$\bar{X}= 28.39\text{mm}$, $s=2.49\text{mm}$, $V=8.77$	$\bar{X}= 20.96\text{mm}$, $s=1.65\text{mm}$, $V=7.87$
TL	$\bar{X}= 51.86\text{mm}$, $s=7.30\text{mm}$, $V=14.08$	$\bar{X}= 50.00\text{mm}$, $s=9.07\text{mm}$, $V=18.14$
SW	$\bar{X}=171.03\text{g}$, $s=21.47\text{g}$, $V=12.55$	$\bar{X}=120.40\text{g}$, $s=12.72\text{g}$, $V=10.56$
BW	$\bar{X}=581.71\text{g}$, $s=85.73\text{g}$, $V=14.74$	$\bar{X}=300.80\text{g}$, $s=79.79\text{g}$, $V=26.53$

Statistical tests for the geographic variation between the Tanon and Fiji areas.

D	$F=1.22 < 4.50=F_{0.05}(\lambda=31, 5)$, $P > 0.05$, not significant $t=6.06 > 2.03=t_{0.05}(\lambda=34)$, $P < 0.05$, significant
B	$F=1.12 < 4.50$, not significant ($P > 0.05$) $t=5.94 > 2.03$, significant ($P < 0.05$)
H	$F=1.64 < 4.50$, not significant ($P > 0.05$) $t=5.35 > 2.03$, significant ($P < 0.05$)
WL	$F=3.69 < 4.50$, not significant ($P > 0.05$) $t=3.25 > 2.03$, significant ($P < 0.05$)
BL	$F=1.23 < 4.50$, not significant ($P > 0.05$) $t=2.22 > 2.03$, significant ($P < 0.05$)
ED	$F=2.28 < 4.50$, not significant ($P > 0.05$) $t=6.41 > 2.03$, significant ($P < 0.05$)
TL	$F=1.54 < 2.53=F_{0.05}(\lambda=5, 31)$, $P > 0.05$, not significant $t=0.51 < 2.03$, not significant ($P > 0.05$)
SW	$F=2.85 < 4.50$, not significant ($P > 0.05$) $t=5.09 > 2.03$, significant ($P < 0.05$)
BW	$F=1.15 < 4.50$, not significant ($P > 0.05$) $t=6.85 > 2.03$, significant ($P < 0.05$)

stage.

Concluding Remarks

The fairly large intraspecific variation in *N. pompilius* expressed by the size or weight

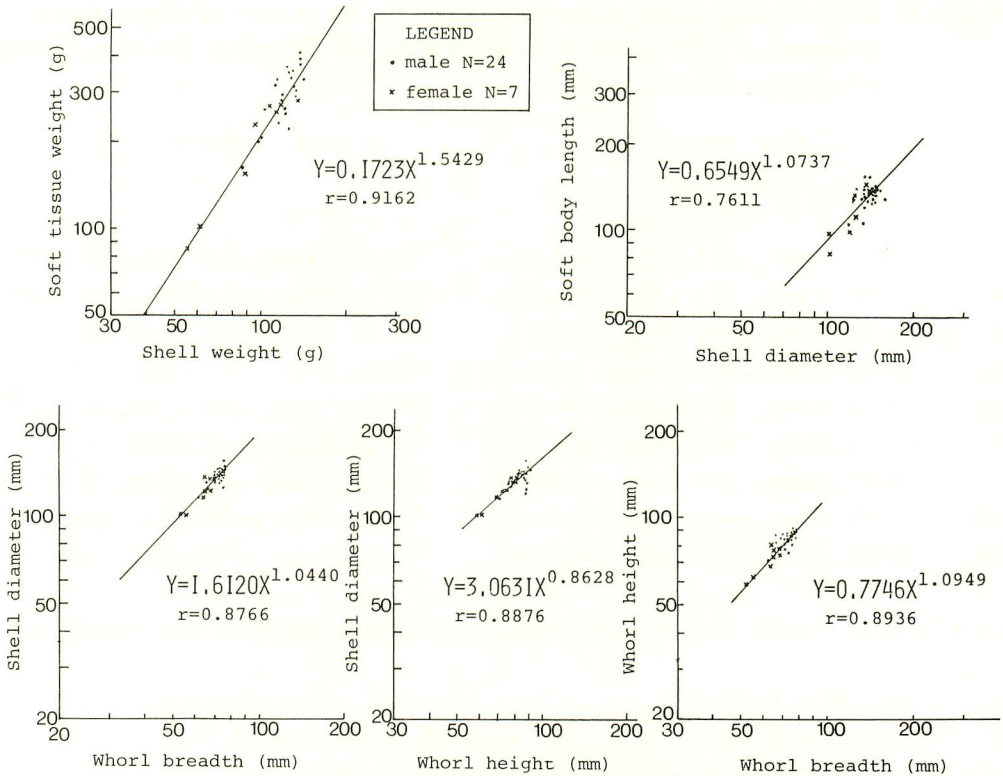


Fig. 3. Double logarithmic scatter diagrams between a pair of several morphologic characters, showing the average relative growth of the specimens from the Fiji area. Regression of Y on X is given in each diagram.

in the mature stage has briefly mentioned by ourselves (HAYASAKA *et al.* 1982). Unfortunately, the variation treated in this paper is the continuous variation of the dimensional variables, which may be controlled by polygenes (MATHER 1949). It is well known that the continuous variation is usually influenced by the environmental factors such as temperature, salinity etc., and food. It is at present unclear that the inter-specific variation realized in this paper is controlled mainly by a genetic factor or environmental ones. However, the fairly large genetic differentiation between the Tañon and Fiji samples, which was analyzed by the electrophoretic patterns of five enzymes (MASUDA and SHINOMIYA, 1983) suggests that the morphologic variation between the mature specimens from the two areas is in part resulted from the geographic variation of gene frequencies.

Concerning the difference in the environmental conditions between the two areas, the water temperature near the trapping locations in Fiji is about 5°C lower than that in Tañon (for details see HAYASAKA *et al.* 1982 and HAYASAKA and SHINOMIYA 1982). In contrast, the dissolved oxygen in the former is about 6-7 ppm. which is much larger than that (2 ppm.) in the latter. These differences in seawater conditions may affect the absolute growth. Further research from population genetical and field ecological points of view should be required to solve the genetic variation and taxonomic relationships of *Nautilus* species.

Table 5. Results of the principal component analysis of the four parameters (B/D, H/D, B/H and D/BL) for the samples of *N. pompilius* from the Tañon and Fiji areas.

Tañon sample					Fiji sample				
N=31					N=31				
Mean vectors [0.495, 0.596, 0.830, 1.094]					[0.515, 0.597, 0.864, 1.062]				
Variance-covariance matrix					Variance-covariance matrix				
$\begin{pmatrix} 0.00014 & 0.00002 & 0.00020 & -0.00029 \\ & 0.00010 & -0.00009 & -0.00003 \\ & & 0.00047 & 0.00043 \\ & & & 0.00740 \end{pmatrix}$					$\begin{pmatrix} 0.00063 & 0.00041 & 0.00050 & -0.00031 \\ & 0.00091 & -0.00058 & -0.00116 \\ & & 0.00163 & 0.00112 \\ & & & 0.01035 \end{pmatrix}$				
Eigen-values $\lambda_1=1.9577, \lambda_2=1.2096, \lambda_3=0.8319, \lambda_4=0.0008.$					$\lambda_1=1.7477, \lambda_2=1.4835, \lambda_3=0.7475, \lambda_4=0.0214$				
Eigenvectors					Eigenvectors				
Variables	1	2	3	4	Variables	1	2	3	4
X ₁	-0.6333	0.1507	-0.6771	0.3432	X ₁	0.4033	0.6796	-0.1765	0.5868
X ₂	0.3069	0.8656	-0.2499	-0.3067	X ₂	0.7125	-0.0083	-0.3752	-0.5924
X ₃	0.3478	0.2428	0.1787	0.8878	X ₃	-0.2916	0.7245	0.2978	-0.5490
X ₄	-0.6202	0.4110	0.6682	-0.0044	X ₄	-0.4947	0.1150	-0.8599	-0.0519
Percentage of variation					Percentage of variation				
48.94 30.24 20.80 0.0002					43.69 37.08 18.69 0.005				
Variation of component scores					Variation of component scores				
Z1: $\bar{X}=-0.0010, s=1.3761$					Z1: $\bar{X}=0.0005, s=1.3004$				
Z2: $\bar{X}=-2 \times 10^{-8}, s=1.0813$					Z2: $\bar{X}=3 \times 10^{-8}, s=1.1976$				
Z3: $\bar{X}=0.0003, s=0.8985$					Z3: $\bar{X}=0.0003, s=0.8509$				

Table 6. Correlation matrix of the dimensional and nondimensional variables in the sample of *N. pompilius* from the Fiji area. For abbreviations of the variables see explanations in the text.

	D	B	H	WL	BL	TL	ED	SW	BW	B/D	H/D	B/H	D/BL	
D	1	<u>0.857</u>	<u>0.867</u>	<u>0.879</u>	<u>0.716</u>	<u>0.699</u>	<u>0.688</u>	<u>0.882</u>	<u>0.809</u>	-0.567*	-0.200*	<u>-0.386</u>	-0.072*	
B		1	<u>0.877</u>	<u>0.781</u>	<u>0.669</u>	<u>0.688</u>	<u>0.859</u>	<u>0.868</u>	<u>0.803</u>	-0.064*	0.090*	-0.157*	-0.172*	
H			1	<u>0.892</u>	<u>0.738</u>	<u>0.725</u>	<u>0.813</u>	<u>0.883</u>	<u>0.893</u>	-0.279*	0.312*	<u>-0.610</u>	-0.265*	
WL				1	<u>0.779</u>	<u>0.665</u>	<u>0.686</u>	<u>0.845</u>	<u>0.819</u>	-0.468	0.071*	<u>-0.561</u>	-0.285*	
BL					1	<u>0.793</u>	<u>0.713</u>	<u>0.801</u>	<u>0.812</u>	-0.329*	0.083*	<u>-0.441</u>	-0.707	
TL						1	<u>0.826</u>	<u>0.782</u>	<u>0.837</u>	-0.245*	0.092*	<u>-0.357</u>	<u>-0.444</u>	
ED							1	<u>0.836</u>	<u>0.797</u>	0.050*	0.294*	-0.242*	-0.326*	
SW								1	<u>0.864</u>	-0.321*	0.061*	<u>-0.392</u>	-0.323*	
BW									1	-0.279*	0.214*	<u>-0.515</u>	<u>-0.429</u>	
Remarks										B/D	1	<u>0.536</u>	<u>0.496</u>	-0.120*
confidence level of correlation coefficient (r)										H/D	1	<u>-0.464</u>	<u>-0.376</u>	
0.349 = r at P=0.05, N=29										B/H	1		0.280*	
0.449 = r at P=0.01, N=29										D/BL	1			
_____ : r is significant at 99% confidence level														
----- : r is significant at 95% c. level but not significant at 99% level.														
* : r is not significant at 95% confidence level.														

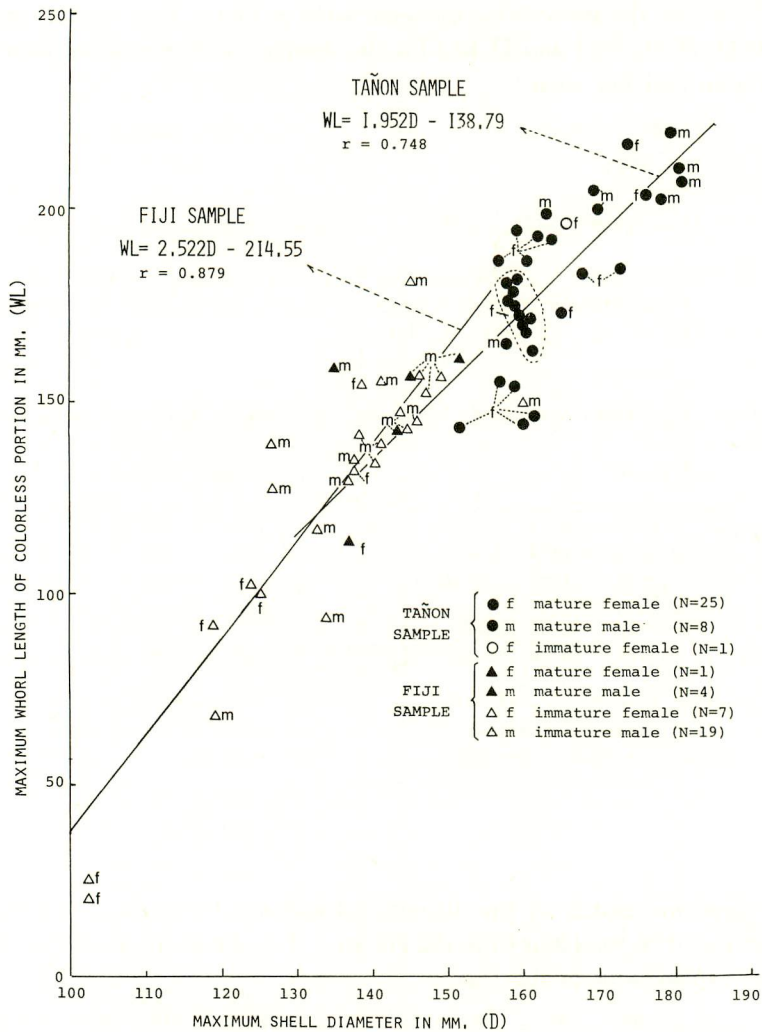


Fig. 4. Double scatter diagram showing the relationship between the maximum whorl length of colorless portion and the maximum shell diameter in the samples from the Tañon and Fiji areas. The regression lines by the least square method are given for the two samples.

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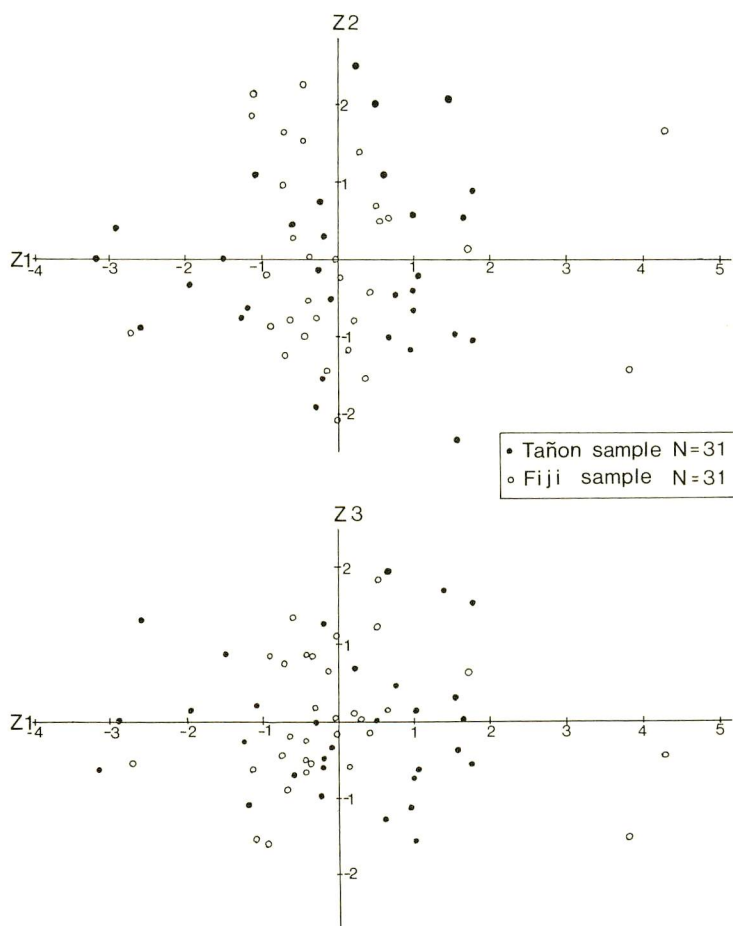


Fig. 5. Plot of the first three principal component scores for the four parameters of form ratio in the samples from the Tañon and Fiji areas.

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