尾虫類 Oikopleura labradoriensis Lohmann の成熟段階と相対成長

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Maturity Stages and Relative Growth of *Oikopleura labradoriensis* LOHMANN (Tunicata, Appendicularia)

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**Abstract**

The state of maturity of *Oikopleura labradoriensis* LOHMANN, which is abundant in the boreal waters, was divided into five stages from juvenile to adult, on the basis of the external characters of the gonad. From the allometric equation used for the interpretation of the changes of body shape, it was shown that the various body parts of the animal did not always increase at the same growth rate during the course of growth. The gonad developed exclusively in the stage subsequent to stage IV.

The body parts were consistently large in size from the Bering Sea, Funka Bay and off Oshoro Bay respectively, over all stages of maturity. The individuals collected from the Bering Sea were remarkably larger than those from the other two areas. In addition, it was demonstrated that the body proportion and number of subchordal cells of *O. labradoriensis* off Oshoro Bay differed from those of the other two areas. At the same time, it was implied that the gonad length/trunk height ratio would be a useful index for determining the maturity stages of this species.

The relationships between the wet weight and dry weight, the dry weight and trunk length, and the dry weight and tail length were calculated. The contraction of body parts of *O. labradoriensis* during preservation was also estimated.

**Introduction**

The Appendicularia grow from juvenile to adult without metamorphosis, and stages of maturity are difficult to distinguish. Despite this difficulty, it is important to know its maturity stages for studying the population dynamics of this animal in the sea.

FENAUX (1963) was first to try to distinguish seriously the maturity stages and to examine the relative growth of some appendicularians captured at Villefranche-sur-Mer on the coast of the Mediterranean Sea. After him, BUCKMANN (1967, 1970, 1972, 1973, 1974) extensively examined several species of *Oikopleura* and *Fritillaria* sampled from various sea areas, near Neapel in the Mediterranean, in the North Atlantic Ocean, in the Arabian Sea and the Patagonian shelf, and determined three maturity stages for them on the bases of the size and shape of their gonad. The population dynamics of *Oikopleura dioica* and *Fritillaria borealis* f. *typica* were intensively studied by WYATT (1971, 1973) in the North Sea, especially by tracing features of their patchiness. The criterion, however, for the identification of the maturity stages of appendicularians is not yet established well.

In the present study, the author will determine the maturity stages of *Oikopleura labradoriensis* occurring abundantly in the boreal waters on the basis of degree of their gonad development and estimate their relative growth. In addition, the comparisons in the body size and

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shape of animals collected from three different areas will be carried out with another index for maturity.

Materials and Methods

Materials that had been collected with vertical hauls of a Norpac net (North Pacific standard plankton net; 45 cm mouth diameter and 180 cm side length (MOTODA, 1957)) with a 0.35 mm mesh aperture, during the cruise 41 of the T. S. "Oshoro Maru III", Hokkaido University, to the northern North Pacific, the Bering Sea and Bristol Bay in June-August 1971, were used for biometrical studies. For comparison with materials taken from other areas, plankton samples were obtained from off Oshoro Bay on the west coast and near the entrance of Funka Bay on the southwestern coast of Hokkaido, in February and March 1972 and from March to May 1973 respectively. These materials were also taken with vertical hauls of the Norpac nets with 0.35 mm mesh aperture in the former and with 0.10 mm mesh in the latter. Completely preserved individuals of Oikopleura labradoriensis were sorted from the samples and stained with borax carmine to examine their body parts. All the plankton samples used for the present study were preserved in about 4% formaldehyde-sea water (STEEDMAN, 1972—equivalent to 10% formalin-sea water commonly used up to date—for a half or a year after sampling.

First, the animal was examined in detail under a microscope and then divided into five maturity stages on the basis of external characters of its gonad. These stages are as follows. The character of each stage is illustrated in Figures 1 and 2.

Stage I (Figure 1): Gonad is absent. The posterior part of the trunk is taken up by the stomach and the intestine. Early in this stage, the margin of the trunk is covered with thick epithelial tissues, which disappear gradually with the progress of growth.

Stage II (Figure 1): A small and thin gonad appears as a testis at the posterior margin of the intestine. The testis is not yet differentiated on the left and right side in the trunk.

Stage III (Figure 1): The gonad increases in height along the posterior margin of the alimentary canal. It is possible to distinguish gonad as two separate testes. The width of the gonad is always less than the width of the alimentary canal—equal to the maximum width of the trunk.

Stage IV (Figure 2): The gonad mainly increases in thickness so that it shows a roundish shape. At the same time it bends and expands to the posterior. The ovary is distinguished from testes and is found between both testes in the posto-dorsal view. The width and height of the gonad are nearly equal to those of the trunk.

Stage V (Figure 2): The well developed, massive gonad occupies the posterior part of the trunk and occasionally covers a part of stomach. Its width and height are always greater than those of the trunk.

Secondly, the body parts of the animal in a certain stage were measured with a micrometer under a microscope. Sometimes, individuals with bent tails or folded fins were present in the samples. Such individuals were straightened carefully with a weak pincette on a
Fig. 1. Maturity stages I, II and III of *Oikopleura labradoriensis*.

a: left lateral view, b: ventral view, c: dorsal view of trunk.
slideglass. As shown in Figure 3, the biometrical characters are (a) length without lower lip, (b) height and (c) width of trunk, (d) length, (e) thickness and (f) width of gonad, (g) length and (h) width with fin of tail, (i) musculature width, and (j) number and shape of subchordal cells. Here, (c) trunk width, and (f) gonad width were measured only for the samples obtained from Funka Bay. Individual numbers measured were 335 for the Bering Sea, 115 for the Oshoro, and 185 for the Funka Bay samples.

![Stage IV and Stage V](image)

Fig. 2. Maturity stages IV and V of *Oikopleura labradoriensis*.

a: left lateral view, b: ventral view, c: dorsal view of trunk.

For the measurement of wet and dry body weight, some individuals collected from the Bering Sea, which had already been measured for body characters as mentioned above, were used. Each specimen was rinsed with distilled water for 6 to 8 hours, and after removing the excess water from its body surface on filter papers, the wet body was weighed with a Mettler H 20 (the minimum weighing 10 µg). Then, the specimen was dried in an oven at 60±1°C overnight, and kept in a desiccator until a constant weight was given. The dry specimen was measured with a Mettler’s ultramicro balance (UM 7; the minimum weighing 0.1 µg). This drying procedure is a standard technique recommended by LOVEGROVE (1966). One hundred and thirty nine specimens were used for the wet and dry body weight measurement.

Finally, the trunk length and/or tail length were chosen as a standard measurement of
body size, and the relationships between the standard measurements and those of various body parts were calculated to study relative growth of various parts of *O. labradoriensis*. The concept of relative growth was proposed by Huxley and Teissier (1936). The allometric equation is expressed as

\[ Y = bX^k, \]

or in logarithmic form,

\[ \log Y = \log b + k \log X \]

where \( X \) is the standard length and \( Y \) is the length of another body part. These two measured variables were plotted on a double logarithmic coordinate, which is a useful procedure to find whether inflection points exist or not, in the relative growth. The equilibrium constant \( k \), and the initial growth index \( b \), in the equation were calculated by the method of least squares. In the above equation, if \( k > 1 \), the allometry is tachyauxesis; if \( k < 1 \), it is bradyauxesis; and in the case where \( k = 1 \), it is isauxesis. The test of significant difference for the allometry of *O. labradoriensis* was carried out by the analysis of covariance. The range of \( k \) was estimated at the 5% level.

![Figure 3](image)

Fig. 3. Measured body parts of *Oikopleura labradoriensis*. (a) length, (b) height and (c) width of trunk; (d) length, (e) thickness and (f) width of gonad; (g) length and (h) width of tail; (i) musculature width; (j) number of subchordal cells.

All the statistical methods were referred to Snedecor and Cochran (1967). Statistical procedures were carried out mostly by means of the SPSS program of Hokkaido University Computing Center.
Results

Relative growth of *Oikopleura labradoriensis*

Though the relative growth of *O. labradoriensis* may be geographically different, the samples from the Bering Sea were used for examination of the relative growth of this animal, because of the greater abundance of individuals than off Oshoro Bay and Funka Bay.

**Table 1. Statistical results in the allometric equation, log \( Y = log b + k log X \), of *Oikopleura labradoriensis* taken from the Bering Sea in June-July, 1971. Test of significant difference was done by the analysis of covariance. All correlation coefficients were significant at the 0.1 % level. Figures in parentheses indicate the 95 % confidence interval of \( k \).**

<table>
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<tr>
<th>Relation</th>
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<th>X</th>
<th>Phase</th>
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<th>log ( b )</th>
<th>r</th>
<th>F-test for slope</th>
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<td>Trunk length</td>
<td>I</td>
<td>192</td>
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<td>0.9669—1.0224</td>
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<td>0.9813</td>
<td>( F=261.34 ) (d. f. =1, 328) ( P&lt;0.001 )</td>
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<td>Trunk length</td>
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<td>2.3076</td>
<td>1.675—2.9400</td>
<td>-4.7550</td>
<td>0.8271</td>
<td>( F=20.03 ) (d. f. =1, 77) ( P&lt;0.001 )</td>
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<td></td>
<td></td>
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<td>53</td>
<td>1.1947</td>
<td>1.0227—1.3667</td>
<td>-1.0672</td>
<td>0.8903</td>
<td>( F=7.88 ) (d. f. =1, 94) ( 0.005&lt; P&lt;0.01 )</td>
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<td>-2.9574</td>
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<td>Tail length</td>
<td>Trunk length</td>
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<td>0.9741—1.1060</td>
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<td></td>
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<td>0.6607—0.7187</td>
<td>0.6897</td>
<td>0.9526</td>
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<td>Musculature width</td>
<td>Tail length</td>
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<td>155</td>
<td>1.1540</td>
<td>1.1129—1.1950</td>
<td>-1.6744</td>
<td>0.9757</td>
<td>( F=20.26 ) (d. f. =1, 275) ( P&lt;0.001 )</td>
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<td></td>
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</tr>
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<td>Tail width</td>
<td>Tail length</td>
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<td>0.7731—1.1142</td>
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<td>1.2127—1.7061</td>
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<tr>
<td>Dry weight</td>
<td>Trunk length</td>
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<td>66</td>
<td>1.7812</td>
<td>1.5796—1.9428</td>
<td>-3.6034</td>
<td>0.9109</td>
<td>( F=5.78 ) (d. f. =1, 123) ( 0.01&lt;P&lt;0.025 )</td>
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<td>1.9260—2.8766</td>
<td>-5.6427</td>
<td>0.7962</td>
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<tr>
<td>Dry weight</td>
<td>Tail length</td>
<td>I</td>
<td>68</td>
<td>1.6714</td>
<td>1.4948—1.8481</td>
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<td>0.9188</td>
<td>( F=13.50 ) (d. f. =1, 125) ( P&lt;0.001 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>II</td>
<td>61</td>
<td>3.1508</td>
<td>2.2883—4.0133</td>
<td>-10.2240</td>
<td>0.6894</td>
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The statistical results in the allometric equation of *O. labradoriensis* are given in Table 1. As shown in Figures 4, 5, and 6, they have one inflection point, except that the gonad length-trunk length has two. All correlation coefficients are significant at the 0.1 % level. Each linear regression was calculated on both sides of the inflection point in the allometric equation. The test of significant difference for the slope between the phases proves to be highly significant in all the relations. In general, all correlation coefficients tend to decrease.
as growth advances, which may suggest that the body parts vary widely with increasing growth.

In the relationship of trunk height to trunk length, there is an inflection point at about 2,340 µm in trunk length. The point exists between maturity stages III and IV. The trunk height indicates isauxesis at phase I and also bradyauxesis at phase II. There are two inflection points, i.e. at 2,000 µm and near 3,200 µm in trunk length, in the relation of gonad length versus trunk length. Phase I, phase II, and phase III are mainly composed of maturity stages II, III and IV, and V respectively. The gonad length shows tachyauxesis over all maturity stages. In the relationship of tail length versus trunk length, an inflection point exists at about 1,600 µm in trunk length, corresponding closely to maturity stage II. The tail length indicates isauxesis and bradyauxesis at phase I and phase II respectively. The
musculature width-tail length shows tachyauxesis at phases I and II. There is an inflection point at 10,000 µm in tail length, which corresponds to the range of the tail length of maturity stage III. Meanwhile, the tail width versus tail length has also an inflection point at 10,000 µm and shows isauxesis at phase I and tachyauxesis at phase II.

In the length-weight relationships (Figure 6), maturity stages I-III and IV-V correspond to phases I and II respectively. That is, an inflection point, though less pronounced, exists between stage III and stage IV. The dry weight against the trunk length shows $k=1.7812$ and $2.4011$ at phases I and II respectively. The dry weight against the tail length gives $k=1.6714$ at phase I and $k=3.1508$ at phase II with a highly significant difference between each other ($P<0.001$).

![Graph](image)

**Fig. 5.** Relative growth of the body parts versus tail length of *Oikopleura labradoriensis*.

The body parts of *O. labradoriensis* do not always change with the same growth rate during the course of growth. This tendency is remarkable in the relationships between body parts and trunk length, because the inflection point is different from each other. The body parts against the tail length have the same inflection point, 10,000 µm in tail length.

The gonad develops exclusively in length at phase I ($k=2.3076$), whereas the length shows weak tachyauxesis ($k=1.1947$) at phase II. This fact may indicate that the gonad increases relatively in thickness than length at phase II. At phase III, it again rapidly grows both in length and thickness, and become massive. The development of tail length is just
opposite to that of the gonad. The growth rates of musculature width and tail width as compared to tail length tend to increase with the growth.

There is a good correlation between the dry and wet weight of *O. labradoriensis* over all maturity stages as follows:

\[
\log Y = -0.0282 + 1.3822 \log X \quad (r=0.9320; \; n=104; \; P<0.01),
\]

where \( X \) is the dry weight and \( Y \) is the wet one in \( \mu g \). The relationships such as wet-dry weight, dry weight-trunk length and dry weight-tail length help in estimate the biomass of this species occurring in the sea, though these relationships may vary between different sea areas. The ratio of dry to wet weight of the species is 15.34 % on the average, widely ranging from 57.11 to 4.26 % with decrease of larger individuals.

![Fig. 6](image-url)

It is generally known that the body weight decreases during preservation in a formaldehyde sea water solution. Therefore, these values obtained are slightly lower than those of fresh materials (AHlstrom and Thrailkill, 1963; Hopkins, 1969; Omori, 1969, 1970).

Body size of *Oikopleura labradoriensis* taken from three different areas

The results of body part measurements of the animals collected at three different areas,
the Bering Sea, off Oshoro Bay and near the entrance of Funka Bay, are presented in Table 2. The minimum body size of *O. labradoriensis* is recorded as 212 µm in trunk length and 950 µm in tail length for the same individual caught from Funka Bay. The maximum trunk length is 4,545 µm with 15,950 µm in tail length. On the other hand, the maximum tail length shows 16,035 µm with 4,000 µm in trunk length. These maximum values in the specimens collected from the Bering Sea are larger than those previously reported (LOHMANN, 1896, 1901, 1905, 1914; TOKIOKA, 1940; BÜCKMANN, 1970).

The sizes of body parts of *O. labradoriensis* are clearly arranged in order of largeness from the Bering Sea, Funka Bay, and off Oshoro Bay at all maturity stages, though data are lacking for stages earlier than stage IV in the samples from Oshoro. In particular, the body size of the Bering Sea's population is approximately twice as large as that of the Oshoro Bay. From the Funka Bay's sample, it is shown that the width of the gonad is smaller than that of the trunk at stages II and III, nearly equal or a little larger at stage IV, and much larger at stage V, respectively.

The ratio of gonad length/trunk height (GoL/TrH) regularly increases in each maturity stage ranging from 0.55 to 1.28 over the three populations, as is shown in Table 2. Therefore, this ratio seems to be a useful index for estimating the maturity of *O. labradoriensis*, regardless of sea area.

The subchordal cells, which are laid in a row at the right of the tail musculature, tend to change shape from flat, triangular, and semicircular to elliptic as the tail length increases. The size of these cells themselves naturally increases with the growth. The number, however, does not clearly increase with the growth, showing a wide range from 9 to 37 cells throughout the whole samples as given in Table 2. The Oshoro Bay's population has obviously a number of the cells lower than the other two populations. TOKIOKA (1940) found 17–25 subchordal cells in the same species sampled from off Shionomisaki in middle Honshu, Japan.

The comparison of the tail length/trunk length (TaL/TrL) ratio of *O. labradoriensis* was carried out to know whether there are significant differences among the three areas or not. The calculation was on the same maturity stage V for each sample. The results and the significant test for the difference of the ratio are given Table 3. The population from Oshoro, having a lower TaL/TrL ratio, is significantly different from the other two populations, as shown by the number of subchordal cells. On the other hand, there is no significant difference in the ratio between the Bering Sea's and Funka Bay's populations.

Fortunately, a small portion of the samples obtained from off Oshoro was measured immediately after sampling. To determine the change of body shape from leaching in the preservative, 32 raw and 66 fixed individuals of the same stage V were used. The test of significant difference was done by the analysis of covariance. In the trunk length-tail length, there was a highly significant difference both in slope (F=9.40; d. f.=1.94; P<0.005) and adjusted mean (F=8.47; d. f.=1.95; P<0.005). This seems to indicate that contraction of the body takes place during preservation. The mean percentage decreases in the length and height of the trunk, in the thickness and length of the gonad, and the length of the tail are
TABLE 2. RESULTS ON BODY PART MEASUREMENTS OF *Oikopleura labradoriensis* TAKEN FROM THREE DIFFERENT AREAS, THE BERING SEA, OFF OSHORO BAY AND FUNKA BAY. VALUES ARE SHOWN AS THE MEAN WITH THE STANDARD DEVIATION OR THE MODE WITH THE RANGE IN PARENTHESES.

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<th>Trunk</th>
<th>Gonad</th>
<th>Tail</th>
<th>Musculature</th>
<th>No. of subchordal cells</th>
<th>GoL/TrH</th>
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<td></td>
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<td>height (TrH)</td>
<td>width (TrW)</td>
<td>length (GoL)</td>
<td>thickness (GoT)</td>
<td>width (GoW)</td>
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<tr>
<td></td>
<td></td>
<td>(±255.0)</td>
<td>(±121.3)</td>
<td>(±29.0)</td>
<td>(±62.9)</td>
<td>(±96.7)</td>
<td>(±110.5)</td>
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</tbody>
</table>
Table 3. Comparison of the tail length/trunk length (TaL/TrL) in stage V of Oikopleura labradoriensis taken from three different areas. Test of significant difference was done by the t-test. Values are shown as the mean with the standard deviation in parentheses.

<table>
<thead>
<tr>
<th>Area</th>
<th>n</th>
<th>TaL/TrL ± Standard Deviation</th>
<th>t-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bering Sea</td>
<td>51</td>
<td>3.960 (±0.247)</td>
<td>(B)-(O): t=4.78, P&lt;0.001</td>
</tr>
<tr>
<td>off Oshoro Bay</td>
<td>66</td>
<td>3.745 (±0.272)</td>
<td>(O)-(F): t=2.86, 0.005&lt;P&lt;0.01</td>
</tr>
<tr>
<td>Funka Bay</td>
<td>59</td>
<td>3.902 (±0.288)</td>
<td>(F)-(B): t=1.06, 0.2&lt;P&lt;0.3</td>
</tr>
</tbody>
</table>

roughly estimated as 18.2 and 10.6, 15.5, and 6.3, and 9.2% respectively. It is reported that volume shrinkage of planktonic animals takes within the first day of preservation (AHLSTROM and THRAILKILL, 1963).

**Discussions**

Recently, PAFFENHÖFER (1973) succeeded in continuously cultivating Oikopleura dioica for as long as 7 months over 19 generations in the laboratory. The generation time of O. dioica was as short as 9.5 days in his study. The neritic species of Oikopleura, such as O. dioica, have a short life span so that it is not of much importance to identify the maturity stages in studies of population dynamics. On the contrary, since O. labradoriensis is regarded as annual (USSING, 1938 quoted by GRAINGER, 1959), the studies on the differentiation of maturity stage is significant for the study of its life history.

It is expected from the results that the gonad development can be used as a parameter of the appendicularian growth. In appendicularians, FENAUX (1963), BÜCKMANN (1967, 1970, 1972, 1973, 1974) and WYATT (1973) also observed maturity stages on the bases of the shape and size of the gonad. According to BÜCKMANN (1970), who determined three stages of maturity for O. labradoriensis, the regression of the "standard trunk length"—equivalent to the trunk length (excluding lower lip) in the present paper—to the length of left stomach lobe was distinctly different at each stage.

In the present study on O. labradoriensis, five maturity stages from juvenile to adult were determined by examining the external characters of the gonad in detail. Here, stages III and IV nearly correspond to the early and late stages of the "Reife B" of the Bückmann's maturity criterion, respectively. The gonad length/trunk height ratio may support the present criterion for dividing the maturity stages, because there is no variability at the same stage for different populations.

The population of the Bering Sea is distinctly larger in body size than those from off Oshoro and Funka Bay, and the population of Funka Bay tends to be larger than that from off Oshoro Bay. BÜCKMANN (1972) also suggested that there was a geographical variation in body size of several appendicularians. Although such variation may come from the difference in the sampling period to some extent, O. labradoriensis has obviously regional variations in adult body size and proportion. The difference in their habitat through the process of ontogeny probably affects the growth rate, and leads to geographical variation. The areas where O.
labradoriensis occurred in the Bering Sea are oceanic regions, while the water off Oshoro and Funka Bay has a neritic character. DEEVEY (1960, 1964, 1966) described the effects of temperature and food on the body length of several marine copepods. McLAREN (1963, 1965) found that the adult size and the generation length of Sagitta elegans and Pseudocalanus are a negative function of temperature, and he (1966) also pointed out that this response to temperature was advantageous to Sagitta elegans in the arctic where food supply is limited seasonally as it is shown from the fecundity and natural mortality.

In addition to the difference in body size of O. labradoriensis, it is expected that the body proportion and number of subchordal cells would change with different localities, because these characters have significant differences between Oshoro Bay and the other two areas. On the other hand, the gonad length/trunk height ratio is constant at each stage for three populations. Thus, the ratio is a useful index for determining the maturity stages of Oikopleura.

Summary

1. The five stages of the maturity of Oikopleura labradoriensis from juvenile to adult, can be distinguished on the basis of external characters of their gonad.

2. The allometric equation showed that the growth rates of various body parts in this species are not always the same throughout the growth. The gonad develops rapidly after stage IV.

3. The size of the body parts is constantly large in the Bering Sea, Funka Bay, and off Oshoro Bay, in order, through the whole maturity stages. The individuals taken from the Bering Sea are remarkably larger than those of the other two areas, and the adult size in the Bering Sea is larger than those previously reported.

4. The ratio of the gonad length/trunk height is a useful index for estimating the maturity of O. labradoriensis.

5. The relationships of wet weight-dry weight, dry weight-trunk length, and dry weight-tail length were presented from specimens in the Bering Sea.

6. The contractions of the body parts of O. labradoriensis during the preservation ranged from 6.3 to 18.2 % in lost length.

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References


