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MATURITY AND GROWTH OF THE PACIFIC GEOUDUCK CLAM, PANOEPA ABRUPTA, IN SOUTHERN BRITISH COLUMBIA, CANADA

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ABSTRACT Measurements were made to determine size and age at maturity and growth of the Pacific geoduck clam, Panopea abrupta, from two areas in southern British Columbia, Canada. Growth rates were slower for P. abrupta from Gabriola Island than those from Yellow Bank. Histological examination of gonads indicated that at sizes <90 mm SL considerably more males matured than females, but at sizes >90 mm SL the sex ratio was similar for males and females. Size at 50% maturity was similar for P. abrupta from both areas (58.3 and 60.5 mm SL, respectively), but age at 50% maturity was slower for geoduck from Gabriola Island (3 y) than those from Yellow Bank (2 y). Although one hermaphrodite was recorded, P. abrupta was considered basically gonochoristic (dioecious).

KEY WORDS: Pacific geoduck, Panopea abrupta, maturity, sex ratio, hermaphrodite, reproduction

INTRODUCTION

The Pacific geoduck clam, Panopea abrupta (Conrad, 1849) (Pelecypoda: Hiattellidae), is distributed along coastal areas from southern California to Alaska and west to southern Japan (Bernard 1983, Coan et al. 2000). Geoduck are found buried up to 1 m deep within soft substrates (e.g., mud and sand) from the low intertidal to at least 100 m (Jamison et al. 1984, Goodwin & Pease 1989). There are commercial fisheries for geoduck in Alaska, British Columbia, and Washington State (Campbell et al. 1998, Bradbury & Taggart 2000, Hand & Bureau 2000). Geoduck are long-lived, reaching ages up to 168 y (Bureau et al. 2002). Adult geoduck have separate sexes and broadcast spawn annually, usually during summer (Andersen 1971, Goodwin 1976, Sloan & Robinson 1984). Planktonic larvae settle on substrates within 47 days, and juveniles burrow into the substrate (Goodwin et al. 1979, Goodwin & Pease 1989). Geoduck juveniles and adults feed by filtering food particles (e.g., phytoplankton) from seawater (Goodwin & Pease 1989). Geoduck growth is variable but most rapid in the first 10 y; thereafter, although growth in shell length is greatly reduced, shell thickness and meat weight continue to increase at a slow rate (Bureau et al. 2002).

Andersen (1971) found 50% maturity occurred at about 75 mm SL in geoduck sampled in the Hood Canal, Washington State, but little is known about the rate of sexual development for P. abrupta, especially in British Columbia. (Sloan & Robinson 1984). The purpose of this paper is to present information on the sexual maturity and growth rates of P. abrupta from two areas in southern British Columbia.

MATERIALS AND METHODS

Samples from as wide a range as possible of P. abrupta were obtained from Yellow Bank, near Tofino on the west coast of Vancouver Island, (Lat. 49°14.18', Long. 125°55.48') during 28 May, 1991 and Gabriola Island, near Nanaimo in Georgia Strait, (Lat. 49°07.6', Long. 123°45.05') during 22 to 23 May, 1991, at depths between 5-15 m for both areas. The clams were transported to the laboratory in coolers (2°C) and kept in running sea water (ambient temperature) until processed within 48 h of capture.

For each geoduck, shell length was measured as the straight-line distance between the anterior and posterior margins of the shell to the nearest mm with vernier calipers. The age of each geoduck was estimated using the acetate peel method of Shaul and Goodwin (1982). Each right valve was sectioned through the hinge plate, the cut surface polished, etched with 1% hydrochloric acid solution for 1.5 mm, washed with distilled water, dried, and an acetate peel made by applying an acetate sheet on the hinge surface with acetone. Growth rings imprinted on the acetate peel were counted on a digitizing table after ×40 magnification using a Neopromar projector. Although most individuals had their SL and age measured, there were some that had only the SL or only the age measured; these latter individuals were included in the analysis where appropriate. Reproductive condition of each geoduck was determined by removing a sample from the central portion of the gonad and preserving the tissue in Davidson's solution (Shaw & Battle 1957). Histological slides were prepared with sections of the gonad stained with hematoxylin-eosin. Histological sections of the gonads were classified into six stages according to Andersen (1971). Stage 0 was immature (no differentiation of gonadal tissue; loose vesicular connective tissue in gonad). The other stages were for mature geoduck (connective tissue well developed, primary cells evident on follicle walls or eggs or sperm development evident) and classified as: (1) early active; (2) late active; (3) ripe; (4) partially spent; and (5) spent.

Average von Bertalanffy growth curves were fitted to all data points of size at age using the equation:

\[ L_t = L_\infty \left( 1 - e^{-k(t-t_0)} \right) \]

where \( t \) is age in years, \( L_\infty \) is shell length (mm) at age \( t \), \( t_0 \) is theoretical maximum size, \( k \) is a constant, determining rate of increase or decrease in length increments, \( t_0 \) is the hypothetical age at which the organism would have been at zero length. The parameters \( L_\infty \), \( k \), and \( t_0 \) were estimated using a non-linear Gauss–Newton least squares method (SYSTAT 2000).

The proportion of mature geoduck (P) at shell length or age (X) was estimated using the equation:

\[ P_X = X \left( 1 + e^{-k(X-X_0)} \right) \]

where A and B are parameters estimated using a non-linear Gauss–Newton least squares method (SYSTAT 2000). Data for both sexes were combined for each of the growth and maturity curve analyses since sex could not be distinguished in the immature sizes.
RESULTS

Growth

The oldest *P. abrupta* collected was 77 y (146 mm SL) from Gabriola Island, and 117 y (154 mm SL) from Yellow Bank. The smallest and largest geoduck, respectively, was 10 mm SL (age unknown; probably 1 y) and 163 mm SL (42 y) from Gabriola Island, and 43 mm SL (2 y) and 180 mm SL (58 y) from Yellow Bank. Growth was fastest in the first 10 y followed by slow growth thereafter for geoduck from both areas (Fig. 1). There was considerable variability of size within each age group. Growth rates of *P. abrupta* from Gabriola Island were slower than those from Yellow Bank (Fig. 1, Table 1).

Gonadal Condition

Immature gonads comprised 10.85% and 12.10% of the total geoduck gonads sampled from Gabriola Island (*n* = 129) and Yellow Bank (*n* = 124, includes three individuals without SL measurements), respectively (Fig. 2). The largest immature geoduck was 80 mm SL (5 y) and 72 mm SL (4 y) from Gabriola Island and Yellow Bank, respectively. There were insufficient data to determine spawning periods because seasonal monthly samples were not collected. However, most mature gonads were in the ripe or partially spent condition for geoduck collected from both areas (Fig. 2). There were no gonads that were spent (gonadal condition 5). This suggested that geoduck spawning had begun at both areas during mid to late May 1991.

Sex Ratio

For geoduck <90 mm SL, in both areas combined, 41.18% were immature, and 54.41% were males (Table 2). The sex ratio for mature geoduck <90 mm SL was predominantly (92.5%) male

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**TABLE 1.**

Von Bertalanffy growth parameters for *P. abrupta* from Gabriola Island and Yellow Bank during May 1991. Values in brackets are approximate 95% confidence intervals.

<table>
<thead>
<tr>
<th>Area</th>
<th>L (±e)</th>
<th>K (±0.020)</th>
<th>t₀ (±0.95)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gabriola Island</td>
<td>129.6 (±4.1)</td>
<td>0.146 (±0.020)</td>
<td>-1.02 (±0.95)</td>
<td>120</td>
</tr>
<tr>
<td>Yellow Bank</td>
<td>147.7 (±5.8)</td>
<td>0.189 (±0.055)</td>
<td>-1.42 (±1.17)</td>
<td>108</td>
</tr>
</tbody>
</table>

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Figure 2. Frequency of gonadal condition stages found in gonads of all *P. abrupta* collected from Gabriola (black bars) and Yellow Bank (hatched bars). Gonads classified as 0 = immature, and mature stages that are 1 = early active; 2 = late active; 3 = ripe; and 4 = partially spent.
### TABLE 2.

Percent of total gonads differentiated into mature males and females and immature *P. abrupta* from Gabriola Island and Yellow Bank during May 1989. One 91 mm SL hermaphrodite was found. N = total number. Includes only individuals with SL measurements.

<table>
<thead>
<tr>
<th>Area</th>
<th>Male</th>
<th>Female</th>
<th>Immature</th>
<th>Hermaphrodite</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;90 mm SL</td>
<td>36.76</td>
<td>5.40</td>
<td>37.84</td>
<td></td>
<td>37</td>
</tr>
<tr>
<td>Gabriola Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow Bank</td>
<td>51.61</td>
<td>3.23</td>
<td>45.16</td>
<td></td>
<td>31</td>
</tr>
<tr>
<td>Total</td>
<td>54.41</td>
<td>4.41</td>
<td>41.18</td>
<td></td>
<td>68</td>
</tr>
<tr>
<td>≥90 mm SL</td>
<td></td>
<td>57.61</td>
<td>42.39</td>
<td></td>
<td>92</td>
</tr>
<tr>
<td>Gabriola Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow Bank</td>
<td>45.56</td>
<td>53.33</td>
<td>1.11</td>
<td></td>
<td>90</td>
</tr>
<tr>
<td>Total</td>
<td>51.65</td>
<td>47.80</td>
<td>0.55</td>
<td></td>
<td>182</td>
</tr>
</tbody>
</table>

with few (7.5%) females for both areas combined. In contrast, geoduck ≥90 mm SL had generally a more equal sex ratio, although males were slightly more abundant than females in the Gabriola Island sample, whereas there were slightly more females than males in the Yellow Bank sample (Table 2).

#### Hermaphroditism

Although most of the histological material of mature *P. abrupta* gonads allowed differentiation between females (follicles with oocytes) and males (follicles with spermatozoa) (Fig. 3) there was one individual that was a hermaphrodite, with a gonad showing both male and female characteristics (Fig. 4). This gonad had some follicles containing only either female or male gametocytes per follicle, and other follicles, which contained spermatozoa and oocytes in the same follicle. The geoduck was 91 mm SL (age was not determined).

#### Maturity

Mean size at 50% maturity was similar for geoduck from Gabriola Island, 58.3 mm SL (55.2–59.4 mm SL, lower and upper 95% confidence intervals, CI), and Yellow Bank, 60.5 mm SL (51.1–64.0 mm SL, 95% CI) (Fig. 5, Table 3). Mean age at 50% maturity was about 1 y slower for geoduck from Gabriola Island, 3.09 y (2.68–3.25 y, 95% CI), than at Yellow Bank, 2.04 y (1.72–2.16 y, 95% CI) for Yellow Bank geoduck (Fig. 6, Table 3). The smallest mature male was 45 mm SL (2 y) and 60 mm SL (2 y), the smallest mature female was 59 mm SL (4 y) and 88 mm SL (2 y), and the largest immature geoduck was 80 mm SL (5 y) and 72 mm SL (4 y), respectively, in the samples from Gabriola Island and Yellow Bank.

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Figure 3. Photomicrographs of *P. abrupta* gonadal tissue cross-sections of (A) Male (×400 magnification) showing spermatozoa-filled follicle surrounded by connective tissue, (B) Female (×400) showing oocyte-filled follicle surrounded by connective tissue.

Figure 4. Photomicrographs of hermaphroditic *P. abrupta* gonadal tissue cross-sections of (A) (×250 magnification), and (B) (×160) showing single follicles containing oocytes and spermatozoa.
DISCUSSION

Our findings indicated that growth rates were faster for geoduck from Yellow Bank than those from Gabriola. Results were similar to those of Burger et al. (1998) and Bureau et al. (2002) who found that geoduck from Georgia Strait were generally smaller than those from the west coast of Vancouver Island. Reasons for the differences in *P. abrupta* growth rates between areas could be attributed to a variety of environmental and biological factors associated with different habitats (e.g., substrate type, temperature, exposure to water surge activity, pollution, food availability, and geoduck density or genetic characteristics) (Breen & Shields 1983, Harbo et al. 1983, Goodwin & Shaul 1984, Goodwin & Pease 1991, Noakes & Campbell 1992, Hoffman et al. 2000, Bureau et al. 2002).

Our examination of gonadal condition suggested that the spawning period for geoduck from both study areas was just beginning in mid to late May 1991. Results agree with other gonadal studies of geoduck, which found the main spawning period was during June and July (Andersen 1971, Goodwin 1976, Sloan & Robinson 1984).

The male:female sex ratio of mature *P. abrupta* found in this study (52:48) was similar to that reported by Goodwin (1976) (53:47) and Sloan and Robinson (1984) (57:43). The high percentage of males in the small sizes (young ages) in this study was

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TABLE 3.

Parameter estimates for equation indicating relationships between proportion that are mature with shell length (SL, in mm) or age (years) of *P. abrupta* from Gabriola Island and Yellow Bank during May 1991. See text for equation formula. Values in brackets are approximate 95% confidence intervals.

<table>
<thead>
<tr>
<th>Area</th>
<th>X</th>
<th>A</th>
<th>B</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gabriola Island</td>
<td>SL</td>
<td>8.512 (±2.741)</td>
<td>0.076 (±0.044)</td>
<td>79</td>
</tr>
<tr>
<td>Yellow Bank</td>
<td>SL</td>
<td>7.224 (±2.314)</td>
<td>0.052 (±0.033)</td>
<td>80</td>
</tr>
<tr>
<td>Gabriola Island</td>
<td>Age</td>
<td>2.956 (±1.551)</td>
<td>0.591 (±0.435)</td>
<td>15</td>
</tr>
<tr>
<td>Yellow Bank</td>
<td>Age</td>
<td>2.397 (±1.540)</td>
<td>0.828 (±0.644)</td>
<td>14</td>
</tr>
</tbody>
</table>

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Figure 6. Age at maturity curves for *P. abrupta* collected from Gabriola Island ("O" solid curve), and Yellow Bank ("X" and dashed curve). Number by each symbol indicates number of individuals per age group. See text for equation for the predictive curve and Table 3 for parameter values.
similar to Andersen's (1971) findings of 94.4% males among geoduck with <100 mm SL.

Our findings indicated the first recording of a *P. abrupta* hermaphrodite. Most bivalve species are dioecious (sexes are separate) although hermaphroditism does occur in some species of this group (Coe 1943, Coan et al. 2000). Factors causing hermaphroditism in *P. abrupta* are unknown. Whether the “simultaneous” hermaphroditism (Coe 1943, Eversole 1989) in this geoduck was fully functional in producing viable eggs and sperm is unknown. However, sexuality of different sizes (or ages) in *P. abrupta* has not been studied extensively. We estimated that only ~1,200 individual gonads have been histologically examined to date from mature *P. abrupta* sampled in Washington State and British Columbia (Andersen 1971, Goodwin 1976, Sloan & Robinson 1984, this study). Andersen (1971) and Goodwin (1976) suggested that *P. abrupta* might be gonochoristic where sex is determined by development with males maturing at a smaller size (earlier age) than females. Although we suspect that hermaphroditism is rare in *P. abrupta*, the probability that some level of protandry, sex reversal, or “simultaneous” hermaphroditism in *P. abrupta* (especially for sizes <100 mm SL) may occur and should be investigated further.

Sexual maturity was variable between *P. abrupta* individuals and sexes. Males started to mature at an earlier age than female geoduck in Yellow Bank than Gabriola Island. Although size at 50% maturity was similar for *P. abrupta* from both areas (58.3 and 60.5 mm SL, respectively) age at 50% maturity was slower for geoduck from Gabriola Island (3 y) than Yellow Bank (2 y). Andersen (1971) found sexual maturity of geoduck to be variable, the smallest sexually mature geoduck to be 45 mm SL, and 50% size at maturity to be 75 mm SL (which Andersen estimated to be an age of 3 y). Our study is the first to show that although size at maturity may be similar for geoduck from two different areas, differences in growth rates may influence the age at which geoduck matures sexually. These findings are similar to some studies of other bivalve species, which suggest that onset of maturity may depend more on size than age (e.g., Nakaoka 1994). However, size and age at sexual maturity can also vary between populations in the same bivalve species (Ponurovsky & Yakovlev 1992, Sato 1994). Variation in environmental (e.g., temperature, current patterns, substrate type, and depth) and biological (e.g., genetics, food supply, growth and mortality rates, predation, and parasitism) factors may affect mortality rates within bivalve populations at different locations (Thompson et al. 1980, Ponurovsky & Yakovlev 1992, Nakaoka 1994, Sato 1994, Taskinen & Saarinen 1999).

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**LITERATURE CITED**


