Population structure and breeding season of the hermit crab *Diogenes brevirostris* Stimpson, 1858 (Decapoda, Anomura, Diogenidae) from southern Mozambique

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Abstract

In this study the population dynamics of the diogenid hermit crab *Diogenes brevirostris* is evaluated focusing on size structure, sex ratio and breeding season. Crabs were randomly taken on a monthly basis from January to December 2003 at Costa do Sol, Maputo Bay, southern Mozambique. A total of 622 crabs was obtained of which 290 were males (46.6%), 170 were non-ovigerous females (27.3%) and 162 were ovigerous females (26.1%). The overall size frequency distribution was unimodal for males, non-ovigerous females and ovigerous females. The overall sex ratio (1:1.15) differed from the expected 1:1 ratio. Sexual dimorphism was evidenced by the larger size attained by males in relation to both ovigerous and non-ovigerous females. Breeding took place year-round with three peaks of spawning (March, August and December). Despite the high reproductive activity, young recruits were scarce in the population. The present results suggest that the study area is suitable for reproduction and growth whereas recruitment may take place in different areas from that occupied by the adults.

Keywords: *Diogenes brevirostris*, hermit crabs, population structure, reproduction

Introduction

Studies on populations generally focus on descriptions of density, size structure, sex ratio and breeding periods that can be compared to other populations of the same species, genus or other taxonomic level. Such comparisons are an important strategy to verify differences among populations and to understand the biological constraints that are shaping the structure of these populations (Branco et al. 2002). Moreover, the study of dominant populations may be very important to elucidate the structure and function of communities. Decapod crustaceans represent a large number of living species that inhabit a wide variety of biotopes, and consequently are a promising field of study because the
establishment of these animals in such diverse habitats derives from the evolution of adaptive strategies (Mantelatto and Sousa 2000). Hermit crabs are anomuran decapod crustaceans that developed strategies to utilize gastropod shells and other types of cavities to shelter the uncalcified abdomen. According to Martinelli et al. (2002), there are currently more than 800 species of hermit crabs worldwide, ranging from the deeper parts of the oceans to intertidal habitats. Despite this high diversity, the population biology aspects of these organisms are still poorly known.

There are many studies on different biological aspects of hermit crabs, mostly related to behavioural characteristics such as the use of gastropod shells and habitat selection in both the field and laboratory (e.g. Tunberg et al. 1994; Mantelatto and Garcia 2000; Turra and Leite 2001). However, studies on population structure of hermit crabs have been conducted for European and Mediterranean (Lancaster 1990; Elwood and Neil 1991; Manjón-Cabeza and Garcia-Raso 1994, 1998; Benvenuto and Gherardi 2001), temperate (Asakura and Kikuchi 1984; Asakura 1987, 1991, 1992, 1995; Imazu and Asakura 1994; Carlon and Ebersole 1995; Pessani et al. 2000), tropical (Kamalaveni 1949; Ameyaw-Akumfi 1975; Bertness 1981; Schiller et al. 1991; Gherardi and Nardone 1997; Nakasone 2001) and South American species (Franzoso and Mantelatto 1998; Bertini and Franzoso 2000; Turra and Leite 2000; Garcia and Mantelatto 2001; Branco et al. 2002; Martinelli et al. 2002).

Breeding seasons of hermit crabs have been frequently described and reveal continuous to seasonal patterns (e.g. Manjón-Cabeza and Garcia-Raso 1998; Turra and Leite 2000; see also Table II in this study). Reproductive activity has been shown to be influenced by the morphology of the shells used by the crabs (Carlon and Ebersole 1995; Turra and Leite 1999; Mantelatto et al. 2002). Moreover, reproductive peaks may vary between populations in response to variation in environmental parameters of a given area.

In southern Africa, studies on hermit crab biology are very few (e.g. Ameyaw-Akumfi 1975; Emmerson and Alexander 1986; Walters and Griffiths 1987; Reddy and Biseswar 1993) and, in particular reference to Mozambique, they have been restricted to behavioural and ecological studies (Barnes 1997, 1999; De Grave and Barnes 2001).

**Diogenes brevirostris** Stimpson, 1858 occurs from Saldanha Bay, Mozambique to Durban (Emmerson and Alexander 1986) and is the most common and fast-moving hermit crab occurring in the intertidal habitats and estuaries of southern Africa (Walters and Griffiths 1987). Very little is known about its biology. Emmerson and Alexander (1986) assessed the patterns of shell utilization, morphometrics and fecundity while Walters and Griffiths (1987) addressed questions related to distribution, abundance and shell utilization in the field and laboratory. Virtually nothing is known about its population biology and breeding.

In this paper, we describe the population structure of *D. brevirostris* from Costa do Sol, Maputo Bay, southern Mozambique with emphasis on size structure, sex ratio, breeding season and recruitment.

**Materials and methods**

This study was conducted in the intertidal area of Costa do Sol, Maputo Bay, southern Mozambique (25°55′S, 32°55′E). Three rivers discharge into the area: Nkomati on the north, Maputo on the southern bank and Umbeluzi flowing through the Espírito Santo estuary. The runoff of these rivers brings large amounts of nutrients into Maputo Bay. The climate in Maputo Bay is tropical with an average yearly temperature of 25°C and an average rainfall of ~1000 mm per year.
Hermit crabs were collected monthly at full moon during one year, from January to December 2003, in low-tide periods. Collection was performed by two people during a period of 1 h, covering an area of 300 m². Almost all hermit crabs were found in small aggregations of five or more in small pools that were regularly searched during the study period. After collection, all individuals were bagged and transported immediately to the Laboratory of Ecology of the University Eduardo Mondlane where they were removed by carefully cracking each shell. Sex was determined based on the presence of gonopores. The cephalothoracic shield length (SL=dorsally, from the tip of the rostrum to the V-shaped groove at the posterior edge) was measured with the aid of Vernier callipers (±0.05 mm accuracy) or under a dissecting microscope equipped with an ocular micrometer. The specimens were grouped in 0.5 mm size-class intervals, from 1.5 to 10.0 mm.

The reproductive activity of the population was assessed as the percentage of females carrying eggs relative to the total number of females collected (Fransozo and Mantelatto 1998; Turra and Leite 2000; Martinelli et al. 2002) and the monthly occurrence of ovigerous females was evaluated through one-way ANOVA followed by Scheffé’s test for multiple comparisons (Sokal and Rohlf 1995). The Chi-square test ($\chi^2$) was used to evaluate sex ratio (M:F) and to compare male and female percentages per month. Data were assessed for normality through the Kolmogorov–Smirnov test and the mean size of individuals was compared by the Student’s $t$ test (Sokal and Rohlf 1995). The occurrence of juveniles (individuals of both sexes smaller than the smallest ovigerous female) characterized the recruitment in the population (Garcia and Mantelatto 2001; Martinelli et al. 2002). Mean ± standard deviation (SD) is presented throughout the text.

**Results**

A total of 622 crabs was sampled from which 290 were males (46.6%), 170 were non-ovigerous females (27.3%) and 162 were ovigerous females (26.1%). Animal size (minimum, maximum, and mean ± SD) was 1.8, 10.0, and 5.29 ± 1.38 mm for males; 1.5, 8.0, and 4.39 ± 1.19 mm for non-ovigerous females; and 3.0, 9.2 mm, and 4.89 ± 1.55 mm for ovigerous females, respectively. Males were on average larger than ovigerous females ($t=4.89, P<0.001$) which were in turn larger than non-ovigerous females ($t=6.38, P<0.05$).

Figure 1 depicts the yearly size frequency distribution for all hermit crabs sampled during the study period. There was a unimodal size distribution with a normal distribution for males (Kolmogorov–Smirnov test, KS=0.040, $P>0.05$), non-ovigerous females (KS=0.032, $P>0.05$) and ovigerous females (KS=0.022, $P>0.05$). The size frequency histograms show a clear prevalence of individuals measuring 3.5–6.5 mm SL. The modal size ranged from 4.5 to 5.5 mm SL for males, non-ovigerous females and ovigerous females (Figure 1).

Monthly size frequency distributions for males, non-ovigerous females and ovigerous females are shown in Figure 2. Major differences can be seen between each demographic category. Males often displayed uni- and bimodal distribution, while non-ovigerous and ovigerous females tended to be largely unimodal. Larger males were scarce from the end of summer to winter (April to July). Moreover, ovigerous females were often larger than non-ovigerous females.

Overall sex ratio (M:F) was 1:1.15 in favour of females and differed from the expected 1:1 ($\chi^2=16.73, P<0.05$). Monthly sex ratios (percentage of males) ranged from 30.3 to 66.7%. The percentage of non-ovigerous females was greater than or equal to that of
ovigerous females for 50% of the year (January, February, April, May, July, and December) (see Table I).

*Diogenes brevirostris* showed continuous reproduction ($F=189.315$, $P<0.05$) with the largest peak of occurrence of ovigerous females in March and lesser peaks in June, August, October, and December. There was a significant decrease in February (Figure 3) (Scheffé’s test, $P<0.05$).

Analysis of juvenile recruitment in the study area (all crabs of both sexes <3.0 mm SL) showed that it occurred with higher incidence from April to July (Figure 2). No juveniles were recorded from August to October and again in December.

**Discussion**

**Population structure**

*Diogenes brevirostris* in Maputo Bay, Mozambique is sexually dimorphic with males being generally larger than both ovigerous and non-ovigerous females. This condition has been well documented in other hermit crab species (e.g. Ameyaw-Akumfi 1975; Asakura 1987, 1995; Lowey 1987; Tunberg et al. 1994; Gherardi and Nardone 1997; Wada 1999;
Population structure and breeding of Diogenes brevirostris

Frequency (%)

January
n = 95

July
n = 44

February
n = 45

August
n = 10

March
n = 96

September
n = 29

April
n = 37

October
n = 43

May
n = 90

November
n = 54

June
n = 30

December
n = 96

Shield length (mm)
Three factors can influence the sexual dimorphism of hermit crabs: (1) the difference in energy available for growth, with males growing more because they do not expend energy in egg production, but use their energy for structural metabolism; (2) the larger reproductive effort exhibited by males may be due to their ability

Table I. *Diogenes brevirostris* Stimpson, 1858: total number and sex ratio of individuals collected monthly at Costa do Sol, Maputo Bay, southern Mozambique.

| Month    | Males | Non-ovigerous females | Ovigerous females | Total | Sex ratio (M:F) | $\chi^2$ |
|----------|-------|-----------------------|-------------------|-------|----------------|---------|
| January  | 25    | 38.5                  | 20                | 30.8  | 20             | 65      | 1:1.60* | 2.16   |
| February | 15    | 33.3                  | 25                | 55.6  | 5              | 45      | 1:2.00* | 1.71   |
| March    | 20    | 51.3                  | 3                 | 7.7   | 16             | 39      | 1:0.95  | 0.23   |
| April    | 22    | 59.5                  | 10                | 27.1  | 5              | 37      | 1:0.68  | 1.31   |
| May      | 40    | 44.4                  | 28                | 31.1  | 22             | 90      | 1:1.25  | 0.09   |
| June     | 20    | 66.7                  | 4                 | 13    | 6              | 20      | 1:0.50* | 2.57   |
| July     | 19    | 43.2                  | 13                | 29.5  | 12             | 44      | 1:1.32  | 0.11   |
| August   | 40    | 57.1                  | 10                | 14.3  | 20             | 70      | 1:0.75* | 1.61   |
| September| 16    | 55.2                  | 4                 | 13.8  | 9              | 29      | 1:0.82  | 0.45   |
| October  | 23    | 53.5                  | 8                 | 18.6  | 12             | 43      | 1:0.87  | 0.43   |
| November | 30    | 46.9                  | 15                | 23.4  | 19             | 64      | 1:1.13  | 0.36   |
| December | 20    | 30.3                  | 30                | 45.5  | 16             | 66      | 1:2.30* | 3.78   |
| Total    | 290   | 46.6                  | 170               | 27.3  | 162            | 622     | 1:1.15* | 16.73  |

*Significantly different from the expected 1:1 sex ratio ($\chi^2$ test, $P<0.05$).

Figure 3. *Diogenes brevirostris* (Stimpson, 1858). Percentage of ovigerous females collected from January to December 2003 at Costa do Sol, Maputo Bay, southern Mozambique. Error bars represent standard deviation. Bars sharing the same letter do not differ statistically (Scheffé’s test, $P>0.05$).
to fertilize more than one female; (3) males of larger dimensions have a greater chance of obtaining females for copulation as a function of intraspecific fights (Abrams 1988). Moreover, smaller growth rates of females would be a consequence of the utilization of relatively small shells and of the higher energy allocation to reproduction in relation to males (Fotheringham 1980; Asakura 1992; Bertini and Fransozo 2000). All these factors can help to determine the size of the local population of *D. brevirostris*.

The global size frequency distribution displayed a unimodal pattern with males reaching larger sizes than non-ovigerous and ovigerous females, with females being abundant in the smallest size classes (SL<5.5 mm) while males outnumbered females in the largest ones (SL>5.5 mm). This condition has been reported in other tropical hermit crabs (Reigada and Santos 1997; Mantelatto and Sousa 2000; Turra and Leite 2000). According to Diaz and Conde (1989), unimodality of size frequency distributions generally characterizes a dynamic equilibrium for a certain population, and the occurrence of slight monthly variations could reflect recruitment pulses, growth and differential mortality rates. However, testing departures from Poisson distributions may be used to support hypotheses of randomness and independence of certain events in time and spatial scales (Sokal and Rohlf 1995).

The overall sex ratio differed from the expected 1:1 proportion. Several causes may lead to this discrepancy, such as differences between sexes in longevity and growth rate, differential migration, mortality and sex reversal. Sex reversal (hermaphroditism) is very common among hermit crabs but the causes governing its occurrence are still poorly known (Turra and Leite 2000). According to Werner (1972), sex ratios differing from the 1:1 are widespread among crustaceans. In hermit crabs, females tend to be more abundant than males (Ameyaw-Akumfi 1975; Imazu and Asakura 1994; Reigada and Santos 1997; Garcia and Mantelatto 2001; Martinelli et al. 2002). Turra and Leite (2000) state that this may be explained by higher mortality acting on males or by habitat partitioning, differential feeding restriction or spatial dispersion between sexes. Also important to address is the search for and utilization of shells, which are a limiting resource that may influence the sex ratio, with males being more successful in obtaining adequate shells in relation to females (Asakura 1992; Mantelatto and Garcia 2000).

In our study there were few juveniles. This observation and the maximum size attained by the specimens may support the hypothesis that recruitment may occur in different habitats from those occupied by adults. As mentioned by Asakura (1991), Fransozo and Mantelatto (1998) and Martinelli et al. (2002), this may occur due to the need for protection and particular food resources. Hazlett (1981a, 1981b), studying a population of *Clibanarius vittatus* (Bosc, 1802) in Florida, reported that this crab can undergo along-shore daily movements which can vary from a half metre to a few hundred metres in a single day. Similar daily movements may be responsible for the variation in the relative abundance of juveniles in the study area. Looking at Figure 2, it can be seen that juveniles recruit mostly during winter (March to June) in the study area. In Maputo Bay, phyto- and zooplankton growth occurs from September to November and a major period of plankton abundance occurs by March due to nutrient accumulation during the winter rainy season (Paula et al. 1998). Thus, the juvenile migration may occur throughout the rainy season. Recently, Litulo (2004) found that the reproductive and recruitment activity of the fiddler crab *Uca annulipes* (H. Milne Edwards, 1837) in Maputo Bay occurs in the rainy season, favouring food supply and larval flux. This may also apply to the population of *Diogenes brevirostris* studied herein, since the study area receives water input and nutrient outflow from three major rivers (see Materials and Methods for site description).
Breeding season

Hermit crabs may display continuous (with or without peaks) or seasonal reproductive patterns (Tunberg et al. 1994; Manjón-Cabeza and García-Raso 1998; Fransozo and Mantelatto 1998; Branco et al. 2002) regardless of the taxonomic group (Table II). For example, *Clibanarius vittatus* (see Lowey 1987; Reigada and Santos 1997; Turra and Leite 2000) and *C. antillensis* (Herbst, 1796) (see Turra and Leite 1999, 2000) show different reproductive patterns in different habitats. This is further evidence of the effects of latitude on the reproductive activity of a species. As noted by Sastry (1983), populations of a given species at different latitudes subjected to particular environmental conditions may display different reproductive patterns. Continuous or wide reproductive periods shown by hermit crabs may be a result of multiple spawnings or asynchrony in reproduction.

Ovigerous females of *Diogenes brevirostris* were found year-round in the study area but with the largest peaks in March, August and December, suggesting a continuous reproductive pattern (Figure 3). A similar pattern was found in *Paguristes tortugae* (Schmitt, 1933) studied by Mantelatto and Sousa (2000) and *Clibanarius antillensis* studied by Turra and Leite (2000). Continuous reproduction is important for the determination of several characteristics of a population such as continuous larval supply and juvenile recruitment, which are important mechanisms to stabilize a population.

In most subtropical and tropical regions, the reproductive activity is more intense during the warmer months, when the food sources are abundant in the plankton (Sastry 1983; Ramírez Llodra 2002).

From the literature (Table II) it is noted that most hermit crabs display seasonal reproduction (78%) rather than continuous. However, both continuous and seasonal reproduction is found in subtropical and tropical areas (here delimited as <23°N and S) and cooler temperate latitudes greater than 23°N and S. It is generally expected that tropical species will breed for longer periods and this may be explained by the narrow variations observed in temperature, rainfall, and nutrient input, which are very important for reproduction and larval growth. Sastry (1983) mentioned that a prolonged breeding period indicates that individuals produce several successive broods during the year or breed asynchronously. A similar reproductive pattern seems to be evident in *D. brevirostris*, since several breeding peaks can be observed during the study period (Figure 2).

According to Turra and Leite (2000), any hypothesis to explain the occurrence of hermit crab populations with seasonal reproductive patterns in the tropics and with continuous patterns in temperate regions may be based on the evolutionary histories of populations, although local factors such as competition and shell use should also be considered when assessing the reproductive traits of a species or population. We recognize the need to be cautious in interpreting this limited breeding data as significant taxonomic and location bias is apparent in Table II. For example, (1) all investigations of the breeding periods of hermit crabs in the family Paguridae are limited to the northern hemisphere; (2) most of the studies (74%) are from the northern hemisphere and extend across a broader range of latitude (6–54°N) when compared to the southern hemisphere (15–27°S); and (3) only 19% of the studies have been carried out on tropical hermit crabs in the first place. A statistical analysis of a more exhaustive data set is required to elucidate any patterns in breeding peaks across latitudes (in both hemispheres) and comparative breeding records for congeners found over a wide range of latitudes should provide the best picture. Both of these approaches are beyond the scope of this paper and are future research directions.

This study constitutes a detailed account of the population biology and reproduction of a tropical hermit crab in southern Africa. Further studies on gonad development, fecundity,
| Species                      | Breeding pattern | Breeding peak          | Study area                      | Reference                      |
|------------------------------|------------------|------------------------|---------------------------------|--------------------------------|
| Coenobitidae                 |                  |                        |                                 |                                |
| *Birgus latro*               | Seasonal         | September–October      | Vanuatu, Indian Ocean (15°S)     | Schiller et al. (1991)          |
| *Coenobita cavipes*          | Seasonal         | May–August             | Okinawa-jima, Japan (25°N)      | Nakasone (2001)                 |
| *Coenobita purpureus*        | Seasonal         | May–September          | Okinawa-jima, Japan             | Nakasone (2001)                 |
| *Coenobita rugosus*          | Seasonal         | May–November           | Okinawa-jima, Japan             | Nakasone (2001)                 |
| Diogenidae                   |                  |                        |                                 |                                |
| *Calcinus obscurus*          | Continuous       | December–February      | Flamenco Island, Panama (8°N)   | Bertness (1981)                 |
| *Calcinus tubularis*         | Seasonal         | August                 | Ligurian Sea, Italy (43°N)      | Pessani et al. (2000)           |
| *Clibanarius albidigitus*    | Continuous       | December–February      | Flamenco Island, Panama         | Bertness (1981)                 |
| *Clibanarius antillensis*    | Continuous       | February–May           | São Sebastião, Brazil (24°S)    | Turra and Leite (2000)          |
| *Clibanarius antillensis*    | Continuous       | November–March         | São Sebastião, Brazil           | Turra and Leite (1999)          |
| *Clibanarius chapini* (= C. tricolor) | Continuous     | January–October        | Tengpobo, Ghana (6°N)           | Ameyaw-Akumfi (1975)            |
| *Clibanarius clopetarius*    | Seasonal         | February–May           | São Sebastião, Brazil           | Turra and Leite (2000)          |
| *Clibanarius senegalensis*   | Continuous       | September–December     | Tengpobo, Ghana                 | Ameyaw-Akumfi (1975)            |
| *Clibanarius virensens*      | Seasonal         | July–September         | Kominato, Japan (35°N)          | Imazu and Asakura (1994)        |
| *Clibanarius vittatus*       | Seasonal         | April–October          | São Sebastião, Brazil           | Turra and Leite (2000)          |
| *Clibanarius vittatus*       | Seasonal         | April–August           | São Vicente, Brazil (24°S)      | Reigada and Santos (1997)       |
| *Clibanarius vittatus*       | Seasonal         | April–September        | Florida, USA (28°N)             | Lowey (1987)                    |
| *Dardanus deformis*          | Continuous       | August–October         | Costa do Sol, Mozambique (26°S) | Litulo (unpublished data)       |
| *Dardanus insignis*          | Seasonal         | September–November     | Santa Catarina, Brazil (27°S)   | Branco et al. (2002)            |
| *Diogenes brevirostris*      | Continuous       | March–December         | Costa do Sol, Mozambique        | Present study                   |
| *Diogenes nitidimanus*       | Seasonal         | March–November         | Costa do Sol, Mozambique        | Present study                   |
| *Diogenes pugilator*         | Continuous       | April–July             | Cadiz, Spain (36°N)             | Manjón-Cabeza and García-Raso (1998) |
| *Loxopagurus loxochelis*     | Seasonal         | June–October           | Ubatuba, Brazil                 | Martinelli et al. (2002)        |
| *Paguristes erythrops*       | Seasonal         | March–September        | Anchieta Island, Brazil (21°S)  | Garcia and Mantelatto (2001)    |
| *Paguristes tortuca*         | Continuous       | March–December         | Anchieta Island, Brazil         | Mantelatto and Sousa (2000)     |
| *Paguristes tripugiloides*   | Seasonal         | November–September     | Pacific Coast, USA (46–48°N)    | Nyblade (1987)                  |
| *Petrochirus diogenes*       | Seasonal         | March                   | Penha, Brazil (26°S)            | Turra et al. (2002)             |
| *Petrochirus diogenes*       | Seasonal         | February–April         | Ubatuba, Brazil                 | Bertini and Fransozo (2000)     |
| Paguridae                    |                  |                        |                                 |                                |
| *Cestopagurus timidus*       | Seasonal         | April–November         | Almeria, Spain (37°N)           | Manjón-Cabeza and García-Raso (1994) |
| *Discorsopagurus schmitt*    | Seasonal         | January–April          | Washington, USA (46–48°N)       | Gherardi and Cassidy (1995)     |
| *Discorsopagurus schmitt*    | Seasonal         | January–May            | Pacific Coast, USA              | Nyblade (1987)                  |
| *Elassochirus gilli*         | Seasonal         | September–May          | Pacific Coast, USA              | Nyblade (1987)                  |
Table II. (Continued.)

| Species                  | Breeding pattern | Breeding peak       | Study area              | Reference                  |
|--------------------------|------------------|--------------------|-------------------------|----------------------------|
| *Elassochirus tenuimanus*| Seasonal         | August–May         | Pacific Coast, USA      | Nyblade (1987)             |
| *Labidochirus splendescens*| Seasonal        | July–April         | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus annulipes*      | Seasonal         | April–August       | Massachusetts, USA (41–43°N) | Carlon and Ebersole (1995) |
| *Pagurus armatus*        | Seasonal         | October–September  | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus beringanus*     | Seasonal         | November–September | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus bernhardus*     | Seasonal         | November–May       | Penzance, England (50°N) | Lancaster (1990)           |
| *Pagurus bernhardus*     | Seasonal         | December–May       | Ards Peninsula, Ireland (54°N) | Elwood and Neil (1991)     |
| *Pagurus capillatus*     | Seasonal         | January–May        | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus caurinus*       | Seasonal         | December–September | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus dalli*          | Seasonal         | November–April     | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus filholi*        | Continuous       | April–July         | Hokkaido, Japan (42–45°N) | Goshima et al. (1998)     |
| *Pagurus geminus* (= *P. filholi*) | Seasonal   | January–June       | Kominato, Japan         | Imazu and Asakura (1994)   |
| *Pagurus granosimanus*   | Seasonal         | October–September  | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus hirsutiusculus* | Seasonal         | November–September | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus kenneryi*       | Seasonal         | January–May        | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus longicarpus*    | Seasonal         | April–May          | Massachusetts, USA      | Carlon and Ebersole (1995) |
| *Pagurus longicarpus*    | Seasonal         | April              | New Jersey, USA (39–40°N) | McDermott (1999)           |
| *Pagurus maclaughlinae*  | Continuous       | September–June     | Florida, USA (27–28°N)  | Tunberg et al. (1994)      |
| *Pagurus middendorfii*   | Seasonal         | November–February  | Hokkaido, Japan         | Wada et al. (1995)         |
| *Pagurus nigrofasciata*  | Seasonal         | May–February       | Hokkaido, Japan         | Goshima et al. (1996)      |
| *Pagurus ochotensis*     | Seasonal         | March–September    | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus pollicaris*     | Seasonal         | April              | Massachusetts, USA      | Carlon and Ebersole (1995) |
| *Pagurus samuelis*       | Seasonal         | November–September | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus stevensae*      | Seasonal         | December–April     | Pacific Coast, USA      | Nyblade (1987)             |
| *Pagurus spp.*           | Continuous       | All year           | Flamenco Island, Panama | Bertness (1981)            |
growth, predation, shell utilization, larval ecology, and morphology are needed to better understand the life cycle of *Diogenes brevirostris* in the study area.

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