LIFE HISTORY CHARACTERISTICS OF
PANDALUS MONTAGUI AND *DICHELOPANDALUS LEPTOCERUS*
IN PENOBSCOT BAY, MAINE

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ABSTRACT

A number of life history characteristics of two species of pandalid shrimp from Penobscot Bay, ME, were inferred from length-frequency and relative abundance data collected on five occasions during a bottom trawl survey in 1980-81. *Pandalus montagui* is a sequential hermaphrodite. Sex transition occurs throughout the year, but most transitional individuals were observed in late March. Most individuals change sex shortly before or after reaching age 2, but some do so either a year earlier or a year later. Ovigerous females were observed from late November through January; eggs are apparently produced during the second, third, and fourth years. Fifteen percent of the 0 age-group caught in the fall of 1980 were females which may never have functioned as males. Growth was rapid in the spring and summer and negligible in the late fall and winter. Females which changed sex at age 1 were larger than females which changed sex a year later. *Dichelopandalus leptocerus* is not hermaphroditic. Ovigerous females were collected primarily in late November and early December. Some females produce eggs during their first and second years, but most do so only during their second year. None of the females caught during this study appeared to be older than age 2; a few large males remained in the population during their third year of life. Females of both species were larger than males of the same age-group, a distinction which was attributed to differences in growth rate and, for *P. montagui*, was associated with earlier sex transition. Larger shrimp of both species migrated down the Bay into deeper water as the winter progressed.

The Pandalidae are a family of boreal, subarctic shrimp composed of 2 genera and about 20 species. Four species (*Pandalus borealis, P. montagui, P. propinquus,* and *Dichelopandalus leptocerus*) are common in offshore waters of the Gulf of Maine (Wigley 1960). Of these, *P. borealis* is the largest, reaching a maximum total length of 17-18 cm (7 in), and has been the object of a directed winter fishery in coastal waters of the Gulf of Maine since the late 1930s (Scattergood 1952) and in coastal and offshore waters since 1958[3]. This species is also exploited commercially on the west coast of North America, in the Canadian Maritime Provinces, on the west coast of Greenland, in the Norwegian and North Seas, and in the northwest Pacific (Balsiger 1981).

Pandalus montagui and *D. leptocerus* are smaller species (maximum length 10 cm or 4 in), which are harvested incidentally with *P. borealis* in the Gulf of

Maine, but have little or no market value because of their size. *Pandalus montagui* is also harvested as an incidental species in the Gulf of St. Lawrence (Balsiger 1981), and for many years was the object of several localized commercial beam trawl fisheries in the southern North Sea and in Morecambe Bay, northwest England, until declining stock sizes led to the demise of the fisheries in the Thames estuary (described by Mistakidis 1957) and Morecambe Bay in the 1950s and 1960s. Warren (1973) described a fishery for *P. montagui* in the Wash on the east coast of England which was still active in the early 1970s. *Pandalus propinquus* is also smaller than *P. borealis* and is generally restricted to deeper water (165-330 m in New England waters according to Wigley 1960); consequently it is rarely taken in Gulf of Maine commercial catches.

Pandalus montagui is differentiated taxonomically into two subspecies: *P. montagui tridens* in the North Pacific and *P. montagui montagui* in the North Atlantic from the Arctic south to the British Isles and Cape Cod (Simpson et al. 1970) or Rhode Island (Rathbun 1929). According to Simpson et al. *P. montagui montagui* is found in estuaries, coastal waters, and offshore in depths of 5 to over 700 m, but is more common in shallow waters (20-90 m); at depths > 90 m it is gradually replaced by *P. borealis*.

Squires (1968) reported that *P. borealis* occurred together with *P. montagui* in depths < 200 m in the Gulf of St. Lawrence and southwest of Newfoundland, but at depths between 200 and 300 m with a smooth detritus bottom and temperatures of 4°-6°C, only *P. borealis* were caught; in colder temperatures (−1° to 3°C) in this same depth range, *P. montagui* were more abundant. *Pandalus montagui* was described as a more eurythermal and eurybathic species than *P. borealis*. Of all the pandalids in the northwest Atlantic, *P. montagui* is the only one which inhabits colder Arctic waters < 1.5°C (Squires 1966). The Atlantic subspecies of *P. montagui* has been the subject of several biological studies (Mistakidis 1957; Allen 1963; Couture and Trudel 1969a, b).

Dichelopandalus leptocerus is distributed in the northwest Atlantic from Newfoundland to North Carolina (Rathbun 1929). It has not been reported from the northeast Atlantic and is rare in the northern Pacific (Squires 1966). During a November 1956 bottom trawl survey in New England waters, *D. leptocerus* was much more widely distributed than *P. montagui* or *P. borealis* (Wigley 1960). *Dichelopandalus leptocerus* was also found over a broad depth range (33-340 m), but was common between 35 and 145 m and at temperatures (in November) of 5°-20°C, whereas *P. montagui* occurred primarily between 70 and 135 m and at temperatures of 6°-10°C. *Dichelopandalus leptocerus* was also collected in areas where bottom sediments contained low, medium, and high quantities of organic matter, whereas *P. montagui* appeared to be associated with sediments with relatively low organic content. Thus, in several ways, *D. leptocerus* appears to have less restricted habitat requirements than *P. montagui* (or *P. borealis*). No detailed biological studies of *D. leptocerus* have been published.

The Maine Department of Marine Resources conducted an exploratory bottom trawl survey to determine the abundance and distribution of pandalid shrimp populations in Penobscot Bay (Figure. 1) during 1980-81. During the course of this survey, biological data were collected from about 10,000 shrimp. The objective of this paper is to describe important life history characteristics of *P. montagui* and *D. leptocerus* in Penobscot Bay (the Bay); these include breeding seasons, female sizes and ages at maturity, sex transition, growth, longevity, and migratory behavior. Aspects of the life cycle and reproductive biology of each species were examined as functions of time of year, depth, and location within the Bay.

METHODS

The survey was conducted over the course of a 12-mo period from late November 1980 to early October 1981. Samples were collected during five distinct periods of time at 19 different stations located from Cape Jellison in the northern end of Penobscot Bay to Mark Island, a distance of about 37 km (23 mi) (Fig. 1). Stations were established at depths ranging from 12 m (40 ft) to 84 m (280 ft) and were located in areas of trawlable bottom. Since a primary objective of the survey was to stimulate commercial shrimp fishing, no attempt was made to randomly select station locations, depths, or sampling times. Attempts were made, however, to return to each station as often as possible so as to determine the seasonal variation in the relative abundance of different sexes, reproductive stages, and size groups of each species at individual locations over the course of the year. Adjacent, well-defined, length groups were assumed to represent successive age-groups.

A total of 45 successful tows (i.e., tows that were not aborted because of bottom obstructions, damage to the trawl, or gear malfunction) were made during the entire survey. Of these, 37 tows which could be assigned to a specific area, depth range, and sampling period were selected for data analysis. Area 1 was defined as the upper Bay, area 2 as west of Islesboro, area 3 as south of Islesboro, and area 4 as east of Islesboro; depth ranges were defined as shallow (12-25 m), moderate (25-50 m), and deep (50-85 m) (Table 1). The distributions of sampling effort between stations by sampling period, area, and depth range are shown in Table 2. No data were

TABLE 1.—Definitions of coded sampling periods, areas, and depth ranges, 1980-81 Penobscot Bay shrimp survey.

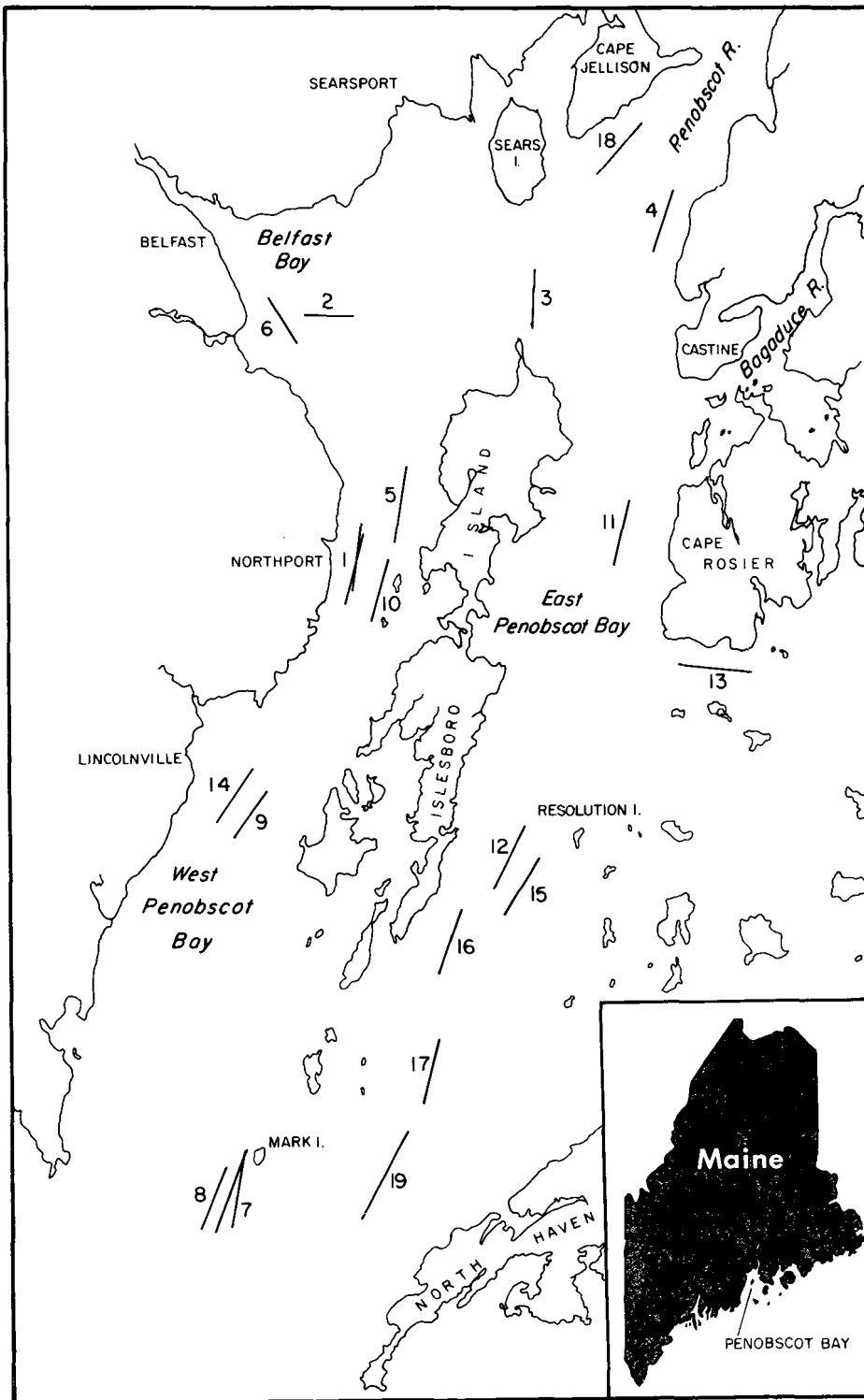| Sampling periods	
1	20 November-2 December 1980
2	21-29 January 1981
3	24-31 March 1981
4	16 July-18 September 1981
5	5-6 October 1981
Areas	
1	Upper Bay: stations 2, 3, 4, 6, 18
2	West of Islesboro: stations 1, 5, 9, 10, 14
3	South of Islesboro: stations 7, 8, 12, 15, 16, 17, 19
4	East of Islesboro: stations 11, 13
Depth ranges	
1	12-15 m (shallow)
2	25-50 m (moderate)
3	50-85 m (deep)

FIGURE 1.—Map of Penobscot Bay, ME, showing bottom trawl stations visited during 1980-81 survey.

TABLE 2.—Distribution of sampling effort (number of tows per station) by sampling period, area, and depth range, 1980-81 Penobscot Bay shrimp survey.[1]

Station	Sampling period					Area				Depth		
	1	2	3	4	5	1	2	3	4	1	2	3
1	2	1		6		9				9		
3	1		1				2				2	
4	1					1				1		
5	1						1				1	
6	1					1				1		
7		1	1		1			3				3
8	1						1					1
9	1		1				2				1	1
10	1	1	3				5				5	
11		1		1					2		1	1
12		1						1				1
13		1							1			1
15		1						1				1
16		1	1		1			3				3
17		1						1				1
18		2					2				2	
19			1					1				1
Totals	9	10	9	6	3	6	17	11	3	6	17	14

[1]See Table 1 for definitions of coded sampling periods, areas, and depth ranges.

available from stations 2 and 14. Trawling operations were limited to the area between Northport and Islesboro in the summer of 1981, since the only vessel available at that time was not equipped to work elsewhere in the Bay.

The trawl used was a semiballoon shrimp try-net with a 7.6 m (25 ft) headrope and 9.5 m (31 ft) footrope with no rollers; mesh size was 38 mm (1½ in) in the body and 31 mm (1¼ in) in the cod end. The trawl was also equipped with a 12.5 mm (½ in) liner. The net was rigged on 1.2 m (4 ft) legs with ark floats on the headrope and 2/0 chain on the footrope. The trawl doors were hardwood, 76 × 41 cm (30 × 16 in), with iron bracings and a wide shoe. The net was fished on a single trawl wire attached to a 30.5 m (100 ft) wire net bridle. All tows lasted 30 min and were made at speeds varying from 1.5 to 2.5 kn. Loran bearings were recorded at the beginning and end of each tow, and depth was recorded either as a single reading or at the beginning and end of each tow. Location and depth could not be determined in the summer since the vessel used then did not have sonar or navigational equipment. Although three different vessels were used during the course of the survey, the gear was identical and was fished the same way during the entire survey.

If catches were small (under 1 kg), the entire catch was generally brought to the laboratory and frozen for later analysis; otherwise, the catch was subsampled aboard the vessel. In some cases, large samples were further subsampled in the laboratory

after they were thawed. Inasmuch as was possible, all samples and subsamples were randomly selected. Samples (or subsamples) of 200-900 g were sorted (after removing extraneous "trash") by species according to morphological characteristics described by Rathbun (1929). Biological data were compiled for a total of 7,259 *D. leptocerus* and 2,475 *P. montagui*; numbers of *P. borealis* were inadequate for data analysis. Each individual shrimp was sexed (male, female, or transitional) using external morphological characteristics for the genus *Pandalus* originally described by Wolleback (1908), Berkeley (1930), Jägersten (1936), and Leloup (1936) and summarized by Mistakidis (1957). The females were further grouped as ovigerous or non-ovigerous depending on whether or not the eggs had "dropped" and were being carried on the pleopods; the non-ovigerous females were further subdivided into two groups— those which had never carried eggs before and those which had—based on the presence or absence of sternal spines. This characteristic of non-ovigerous females was originally described by McCrary (1971) for three pandalid species (*Pandalus borealis, P. goniurus*, and *P. hypsinotus*) in Alaska. Stage I females were defined as those which had not carried eggs before and Stage II females as those which had; there was no way to distinguish between females which had carried eggs only once before and those which had carried eggs more than once. Carapace lengths were measured between the eye socket and posterior dorsal edge of the carapace and recorded to the nearest 0.1 mm.

For each species, the numbers and lengths of shrimp in each biological category (sex, with or without eggs, Stage I or II) were compiled by sampling period, geographic area, and depth range. Length frequencies were expressed as numbers of shrimp per 0.5 mm dorsal carapace length. Since nearly all of the samples collected in areas 1-3 were also collected in specific depth ranges (i.e., all 6 samples from area 1 were from shallow water, 16/17 samples from area 2 were from moderate depths, and all samples from area 3 were from deep water), length frequencies were presented for appropriate area/depth combinations. Length-frequency data for *P. montagui* collected in October 1981 were not presented since so few individuals were captured.

RESULTS AND DISCUSSION

Breeding Seasons and Female Sizes (Ages) at Maturity[4]

Nearly all the ovigerous female *D. leptocerus* were

caught in November-December 1980 (Table 3), although a few remained in January and March. It was therefore apparent that most eggs hatched during a relatively short period of time in late December and early January. Although only the larger size group was carrying eggs (Fig. 2D), the presence of a

were reported for the same populations as late February through April with peak activity in April. According to Couture and Trudel (1969b), ovigerous females were observed in Grand-Rivière, Quebec, beginning in July and accounted for the greatest percentage of the population in October (no samples

TABLE 3.—Percent total number of male and female *Dichelopandalus leptocerus* collected at all locations and depths in Penobscot Bay during five sampling periods in 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	11/20-12/2 1980	1/21-1/29 1981	3/24-3/31 1981	7/16-9/18 1981	10/5-10/6 1981	Total
Total males	49.7	65.3	59.4	47.6	53.0	53.2
Females/Stage I	32.0	33.5	37.8	50.2	45.3	38.8
Females/Stage II	1.4	0.3	1.5	2.2	1.5	1.5
Total non-ovigerous females	33.4	33.7	39.3	52.4	46.8	40.2
Ovigerous females	16.8	1.0	1.3	0.0	0.2	6.6
Total females	50.3	34.7	40.6	52.4	47.0	46.8
Total no. individuals	2,694	729	1,151	1,107	1,577	7,259

few Stage II non-ovigerous females in roughly the same size range (Fig. 2C) indicated that some females produced eggs a year earlier as well. It could not be determined from the samples collected during this study whether the younger females spawned earlier or later than the older group. The fact that so few Stage II females were captured in the Bay at any time of year indicated that most of the spawning population was made up of first time spawners. Ovigerous females were collected at all depths and in all areas (Tables 4, 5), but made up a greater percentage of the catch at moderate depths in area 2.

Nearly all of the ovigerous female *P. montagui* were collected in November-December and late January (Table 6); the fact that 50% of the females in late January were still ovigerous suggests that eggs hatched over a more prolonged period then was true for *D. leptocerus*, possibly from November at least through February. Females belonging to two North Sea *P. montagui* populations were reported to carry eggs primarily between November and February (Mistakidis 1957; Allen 1963), although ovigerous females were observed from mid-October to April in the Thames estuary by Mistakidis. Hatching times

TABLE 4.—Percent total number of male and female *Dichelopandalus leptocerus* collected at all depths and times of year in four areas in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Area 1	Area 2	Area 3	Area 4	Total
Total males	54.4	49.3	57.4	70.6	53.0
Females/Stage I	42.2	39.7	36.7	26.1	38.9
Females/Stage II	1.0	1.8	1.1	1.1	1.4
Total non-ovigerous females	43.2	41.5	37.8	27.2	40.3
Ovigerous females	2.4	9.2	4.8	2.2	6.6
Total females	45.6	50.7	42.6	29.4	47.0
Total no. individuals	1,047	3,626	2,419	92	7,184

TABLE 5.—Percent total number of male and female *Dichelopandalus leptocerus* collected in all areas and times of year by depth range in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Shallow (12-25 m)	Moderate (25-50 m)	Deep (50-85 m)	Total
Total males	54.4	47.7	60.3	53.3
Females/Stage I	41.5	40.4	32.4	37.6
Females/Stage II	1.1	2.0	0.9	1.4
Total non-ovigerous females	42.6	42.4	33.3	39.0
Ovigerous females	3.0	9.9	6.4	7.7
Total females	45.6	52.3	39.7	46.7
Total no. individuals	812	3,015	2,299	6,126

[4]Since no internal sexual characteristics (such as oocyte development) were examined in this study, the breeding season was defined as the period of time when ovigerous females were observed and sizes (ages) at maturity as the sizes (ages) when females produce eggs. No comparable information for males (i.e., mating times or sizes (ages) at maturity) was available. As used in this paper, the breeding season was, strictly speaking, the period of time between spawning and hatching when eggs were incubated.
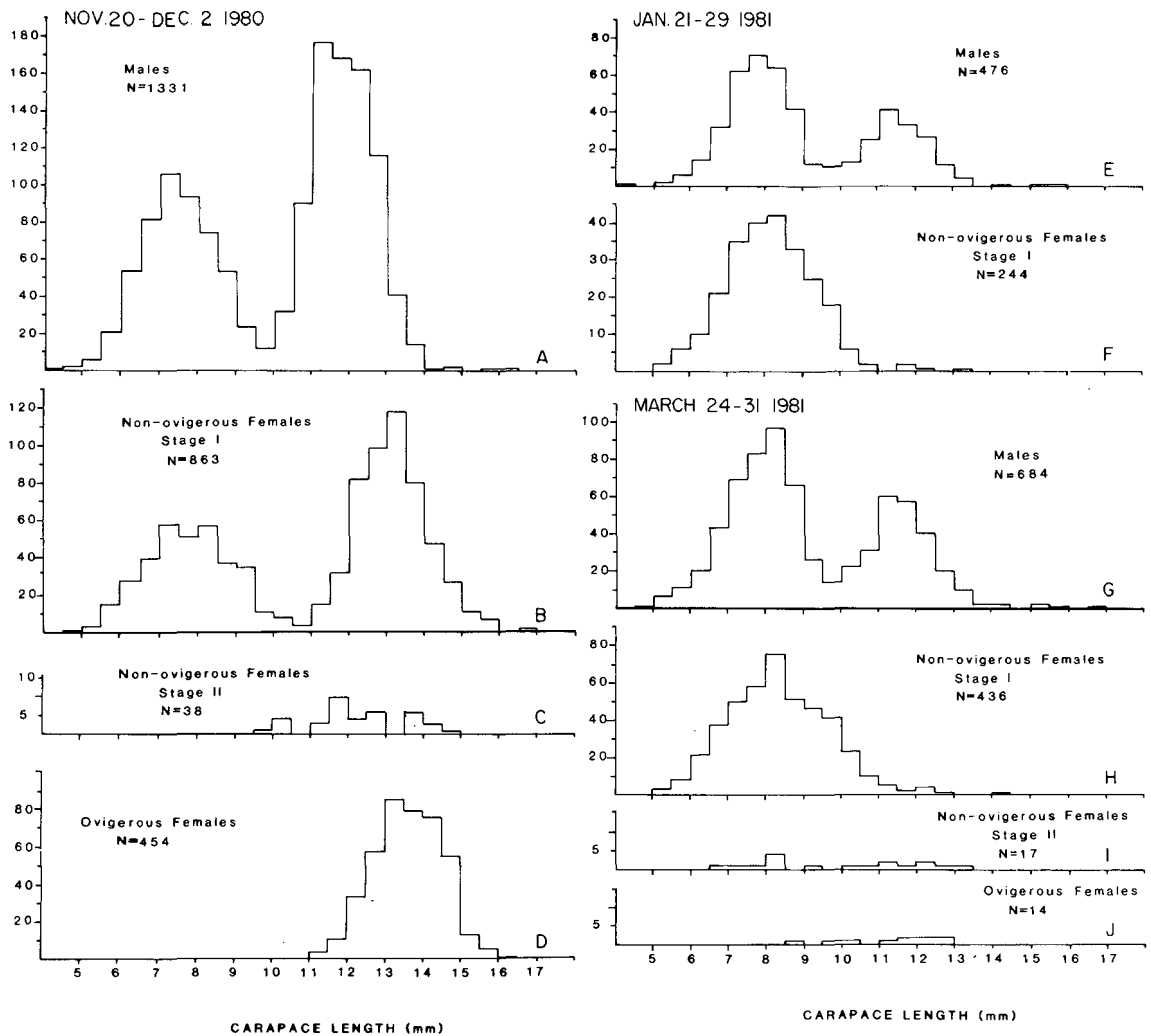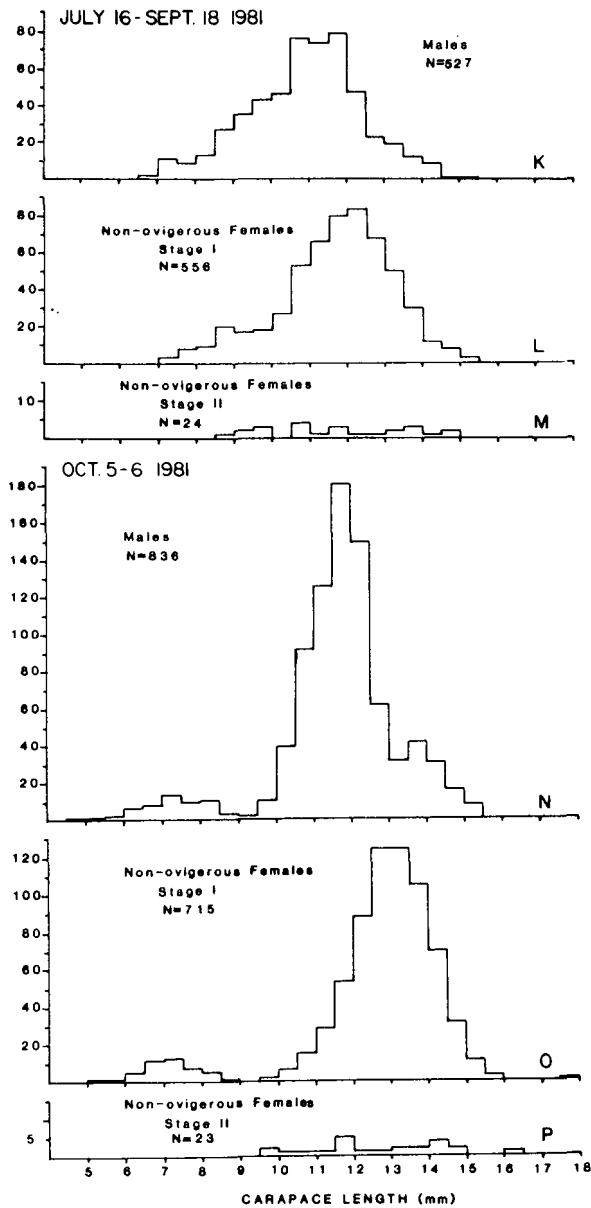
FIGURE 2.—*Dichelopandalus leptocerus* numerical length-frequency distributions by sex and reproductive stage.

TABLE 6.—Percent total number of male, transitional, and female *Pandalus montagui* collected at all locations and depths in Penobscot Bay during five sampling periods in 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	11/20-12/2 1980	1/21-1/29 1981	3/24-3/31 1981	7/16-9/18 1981	10/5-10/6 1981	Total
Total males	73.2	85.2	68.4	37.3	34.3	68.9
Transitionals	0.3	2.5	15.4	5.7	1.5	6.9
Females/Stage I	7.8	6.1	15.9	50.4	61.2	18.2
Females/Stage II	0.3	0.0	0.0	6.7	3.0	1.2
Total non-ovigerous females	8.1	6.1	15.9	57.0	64.2	19.4
Ovigerous females	18.4	6.2	0.4	0.0	0.0	4.8
Total females	26.5	12.3	16.2	57.0	64.2	24.2
Total no. individuals	332	871	800	405	67	2,475

JULY 16 - SEPT. 18 1981

Males
N=527

K

Non-ovigerous Females
Stage I
N=556

L

Non-ovigerous Females
Stage II
N=24

M

OCT. 5-6 1981

Males
N=836

N

Non-ovigerous Females
Stage I
N=715

O

Non-ovigerous Females
Stage II
N=23

P

CARAPACE LENGTH (mm)

were collected between November and April). A few females were still carrying eggs the following June. Hatching began in the winter and continued through June. *Pandalus montagui* populations studied in Penobscot Bay and Grand-Rivière spawned primarily in their second and third years. Females in the North Sea, on the other hand, were fully mature during their first year (Mistakidis 1957; Allen 1963), but there was no evidence that individual age-groups spawned more often there than at Grand-Rivière or in Penobscot Bay.

At least two age-groups of ovigerous *P. montagui* were apparent in the winter samples (Fig. 3C, G), whereas only a single age-group of ovigerous *D. leptocerus* was observed (Fig. 2D). Length-frequency data suggested that older female *P. montagui* (age 2 +) spawned before younger females (age 1); 57% of the ovigerous females collected in November-December were > 15 mm CL (Fig. 3C), whereas only 30% remained in the same size group in late January (Fig. 3G). Sample sizes were much too small, however, to clearly indicate how many spawning age-groups were present or whether older females spawned earlier than younger ones. Earlier completion of spawning by older females was reported by Mistakidis (1957) in the Thames estuary. In Penobscot Bay, the relative abundance of ovigerous females was higher in moderate and deep waters and in areas 2, 3, and 4 (Tables 5, 6).

The capture of a single 10 mm CL ovigerous female *P. montagui* in January (Fig. 3G) indicates that a few females mature and reproduce during their first year. This shrimp could have started life as a female or could have changed sex in the first year and therefore never functioned sexually as a male. Mistakidis (1957) reported that some 0 age-group males in the Thames estuary changed sex and functioned as females during their first year. Some individuals in both the Thames estuary and Northumberland began life as females and matured in their first year (Mistakidis 1957; Allen 1963).

Sex Transition

Unlike most other Pandalid species, the Penobscot Bay population of *D. leptocerus* was not hermaphroditic. Not a single transitional individual was identified in the over 7,000 shrimp which were examined. Furthermore, males and females recruited to the > 5 mm CL population in October of their first year in nearly equal numbers (Fig. 2N, P). The ratio of males to females for the entire survey period was 53:47 (Table 3). *Pandalus montagui*, on the other hand, is a protandric (sequential) hermaphrodite. Nearly 7% of the 2,475 individuals examined exhibited external morphological characteristics typical of transitional *P. borealis* (Allen 1959). The sex ratio was 69% males to 7% transitionals to 24% females (Table 6). Although *P. montagui* is clearly protandric, some individuals in Penobscot Bay either begin life as females or assume external female characteristics by late November of their first year.[5] These

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[5] Individuals of protandric pandalid shrimp species which begin life as females are referred to as primary females; those which change
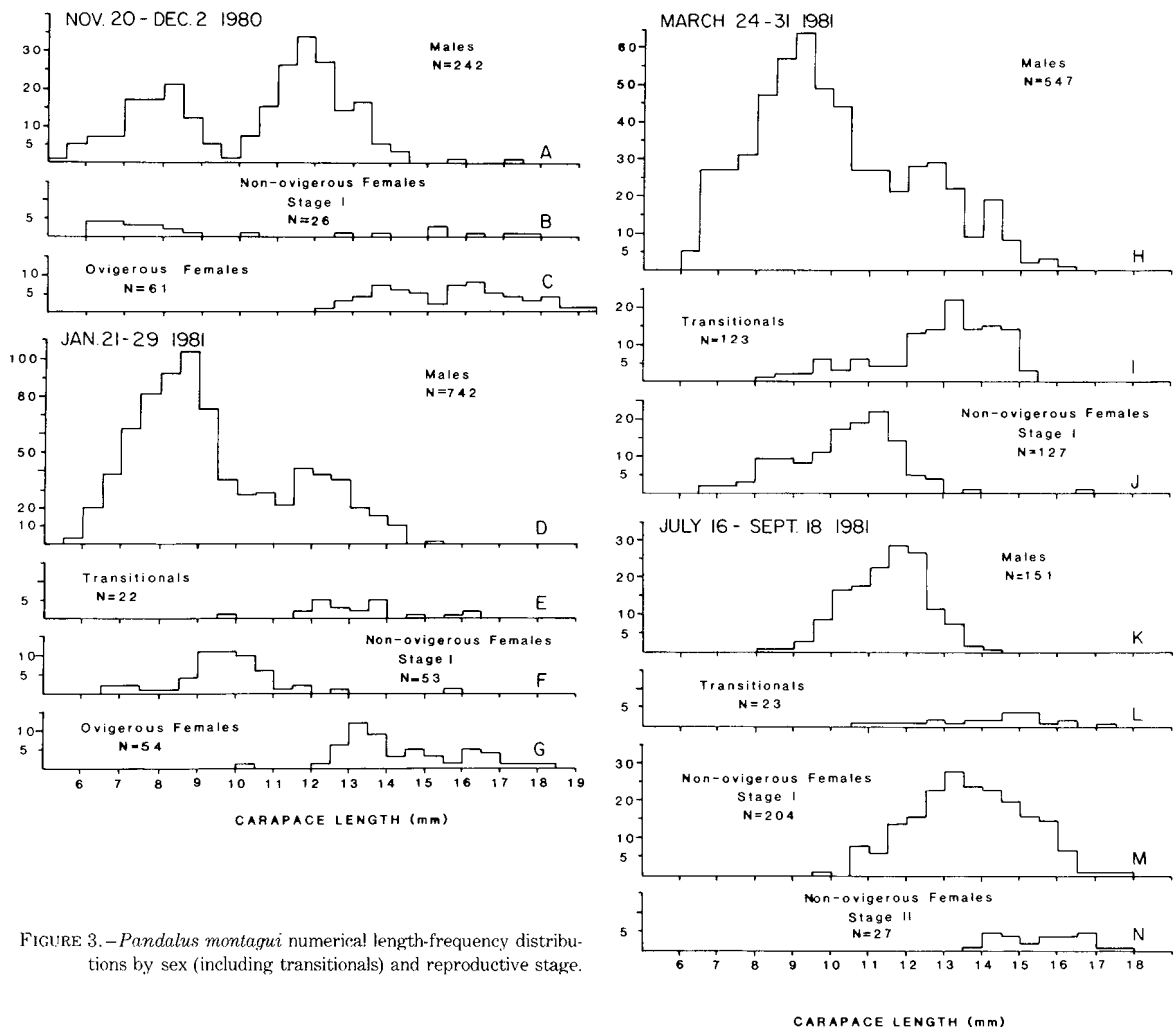
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FIGURE 3. — *Pandalus montagui* numerical length-frequency distributions by sex (including transitionals) and reproductive stage.

females were obvious as a distinct size-group in the November-December length-frequency data at 6-9 mm CL (Fig. 3B). At this time, these females made up 15% of the newly recruiting 0 age-group. The relative abundance of 0 age-group females was considerably higher in the North Sea: 29-37% of most samples in the Thames (Mistakidis 1957) and about 50% in Northumberland (Allen 1963). On the

other hand, only 11.2% of the age-1 *P. montagui* collected in May 1965 in Grand-Rivière were females (Couture and Trudel 1969b).

Size (Age) at Sex Transition

Transitional *P. montagui* were collected during all five sampling periods, but were most abundant in late March (Table 6) following the end of the breeding period. Sex transition apparently began in January, peaked in late March, and continued through the summer and early fall, reaching a minimum in late November. The rapid decline in the relative abundance of males after January 1981 and the accompanying increase in females after March (Table 6) indicated that shrimp, which functioned as males in the previous breeding season and became

sex in their first year following the repression of male sex characteristics and never function as males are called secondary females; and those which function first as males and then change sex are called hermaphroditic females (Mistakidis 1957). Since no distinction could be made in this study between the three types of female *P. montagui*, we have avoided the use of this terminology altogether and simply distinguish between individuals which remained as males during their first year, those which were females when they were first captured in November-December of their first year, and those which apparently changed sex during their first winter.

females prior to the subsequent breeding season, assumed external female characteristics during the winter and spring. The appearance of a distinct size-group of 9-11 mm CL females in late January (Fig. 3F) which was not present 2 mo earlier (Fig. 3B), suggests that transition was well underway by late January. The two size-groups of non-ovigerous females in January and March (Fig. 3I) were assumed to belong to the same age-group, the smaller females being those which did not function as males in their first year (they may have started life as females) and the larger females being those which were still males in November-December (Fig. 3A). Transitional shrimp made up a larger percentage of samples collected in moderate and deep waters and in areas 3 and 4 (Tables 7, 8).

Transition of the younger age-group which˙was first captured in November-December (Fig. 3A) was incomplete since a great many shrimp remained as males for another entire year before undergoing

TABLE 7.—Percent total number of male, transitional, and female *Pandalus montagui* collected at all depths and times of year in four areas in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Area 1	Area 2	Area 3	Area 4	Total
Total males	82.3	63.4	67.1	77.9	68.1
Transitionals	1.6	3.0	11.5	12.3	7.1
Females/Stage I	14.0	25.4	16.8	5.5	18.8
Females/Stage II	0.0	2.6	0.4	0.0	1.3
Total non-ovigerous females	14.0	28.0	17.2	5.5	20.0
Ovigerous females	2.2	5.7	4.2	4.3	4.7
Total females	16.1	33.6	21.4	9.8	24.8
Total no. individuals	186	1,037	827	326	2,376

TABLE 8.—Percent total number of male, transitional, and female *Pandalus montagui* collected in all areas and times of year by depth range in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Shallow (12-25 m)	Moderate (25-50 m)	Deep (50-85 m)	Total
Total males	82.4	61.6	75.3	68.7
Transitionals	1.1	5.8	7.1	5.9
Females/Stage I	14.2	24.0	10.9	18.1
Females/Stage II	0.0	2.7	0.1	1.5
Total non-ovigerous females	14.2	26.6	11.1	19.6
Ovigerous females	2.3	5.9	6.6	5.8
Total females	16.5	32.6	17.6	25.4
Total no. individuals	176	1,013	732	1,921

transition during their third spring (at age 2). Given the fact that a few male and transitional shrimp > 15 mm CL were sampled at various times of year, the possibility that a few individuals do not change sex until their fourth year (age 3) could not be ruled out. Even though the transition of younger (age 1) shrimp in the spring was incomplete, a sizable number of non-ovigerous Stage I shrimp which completed transition in their first year were collected in March (Fig. 3J). These new females were considerably larger (by about 2 mm CL) than their male counterparts, suggesting that it was the larger, faster growing, individuals which underwent transition at age 1. Allen (1963) also reported that the largest 0 age-group males changed sex first.

Older shrimp which changed sex in their second year had not yet appeared as females in March (Fig. 3J), suggesting that sex transition in older shrimp was delayed; it may also have been less rapid, particularly since growth was considerably reduced after the first year. Earlier studies of *P. montagui* indicated that sex transition in two locations in the North Sea persisted for most or all of the year. Mistakidis (1957) noted that sex transition occurred from May to December in the Thames estuary whereas Allen (1963) collected transitional individuals throughout the year in Northumberland, but primarily in June. The timing of minimal sex transition in Penobscot Bay and Northumberland was identical (November-December); Allen (1963) reported that this was when males were sexually active. Couture and Trudel (1969b) reported that most sex transition occurred in October at Grand-Rivière; a few transitionals were collected in July and August but none in May and June. Sex transition in the North Sea, as reported by Mistakidis (1957) and Allen (1963), was accelerated in comparison with Penobscot Bay; some individuals changed sex in their first year, but most did so in their second year. Ages at sex transition at Grand-Rivière, on the other hand, were the same as in Penobscot Bay, i.e., some in their second year, most in their third year, and some in their fourth year.

Seasonal Changes in Size (Age) Composition

Two size-groups of male *D. leptocerus* were observed in the Penobscot Bay during the winter (Fig. 2A, E, G) and only one in the summer (Fig. 2K); similarly, female length-frequency distributions in November-December were bimodal (Fig. 2B), but a single size-group was dominant in the summer (Fig. 2L). Presumably, most of the older (age 2) males either die or migrate out of the upper Bay in the

spring since the younger age-group made up the entire population in the summer. Most of the females apparently spawn once and die after their eggs are hatched since very few older females were found in the winter. The presence of a few larger males in October (Fig. 2N) suggested that a few survive into their third fall and mate twice (or three times if they mature during their first year). Further evidence that most female mortality occurs following hatching while male mortality is delayed until later in the spring was indicated by the seasonal changes in relative abundance of males and females (Table 3): females decreased from 50 to 35% of the population between early December and late January while males decreased more slowly from 65% in January to 48% in the summer.

Age-2 *P. montagui* which were either in transition or were still males in March had mostly become females by the summer (although a few transitionals and large males still remained). The single large size-group of first-maturing Stage I females in the summer (Fig. 3M) presumably included age-1 females at a modal length of 13 mm CL and age-2 females at about 15 mm CL. At the same time, there appeared to be at least two size-groups of Stage II females in July-September (Fig. 3N) which had carried eggs the previous winter (Fig. 3C, G). Ovigerous females captured in November-December 1980 (Fig. 3C) presumably included first-time spawners at 12-15 mm CL and one or two groups of repeat spawners at 15-19 mm CL. Excluding the single female at 10 mm, two or three age-groups of ovigerous females were apparent in January (Fig. 3G). As indicated earlier, the relative abundance of the different age-groups in November-December and January showed that repeat spawners may have accounted for a larger percentage of the ovigerous females earlier in the winter.

Growth and Longevity

Male and female *D. leptocerus* which hatched in the winter of 1979-80 reached 6.0-8.5 mm CL by October of their first year (Fig. 2N, P) and grew relatively slowly during their first winter; by March they had reached 7-10 mm CL and the females were slightly larger than the males (Fig. 2G, H). This difference in size-at-age was also discernible in January (Fig. 2E, F). Growth was rapid during the spring of the second year prior to the beginning of the breeding season: males increased about 3 mm in carapace length by the summer while females increased by 4 mm (Fig. 2K, L). The difference in modal lengths between males and females had increased further by October

(Fig. 2N, P) as growth increased modal carapace lengths by an additional 0.5-1.0 mm for both sexes. Growth between early October and late November when ovigerous females were first sampled was negligible, if October 1981 data can be compared with November 1980 data. During this same short period of time the relative abundance of the younger, newly recruited, age-group (males and females) increased dramatically. (A reduction in somatic growth can be expected at a time of rapid egg development since female growth ceases once their eggs have "dropped" and they are unable to molt). This species reached a maximum observed size of 19 mm CL (not included in compiled length frequencies), but most individuals did not exceed 16 mm CL. Unless older individuals migrate completely out of Penobscot Bay and were therefore not sampled during this survey, the maximum lifespan of *D. leptocerus* in the Bay appears to be about 2 yr and 9 mo, although the bulk of the population apparently survives for only 2 yr.

The first evidence of newly recruited 0 age-group *P. montagui* was in November-December 1980 (Fig. 3A, B). Individuals which remained as males during their second year grew from about 7-9 mm CL in November-December of their first year to 8-10 mm CL in March (Fig. 3H) and 10-13 mm CL in their second summer (Fig. 3K). As was observed for *D. leptocerus*, the growth rate increased in the spring. Age-1 shrimp which became females during their second spring reached 10-12 mm CL in March (Fig. 3J) and 12-15 mm CL in the summer (Fig. 3M). Comparison of November-December 1980 and January 1981 data (Fig. 3C, G) with summer 1981 data suggested that growth of mature females in the fall was negligible; the same was true for the males. The maximum observed size was 19.5 mm CL; females as large as 17-18 mm CL were collected in the winter (Fig. 3C, G). These results suggested that *P. montagui* in Penobscot Bay normally spend 1-2 yr as males and as many as 3 yr as females. The maximum lifespan is probably 4 yr since shrimp that remain males for 2 yr do not complete sex transition until their third year and function as females in their third and fourth years.

Growth at Grand-Rivière was sufficiently slower that males there were 2-3 mm CL smaller by the end of their first year than they were in Penobscot Bay. This difference in growth could be a result of lower summer bottom temperatures in the Gulf of St. Lawrence. A temperature range of $-1°C$ (in May) to $3°C$ (in October) was reported in 54 m at Grand-Rivière in 1965 (Couture and Trudel 1969a). Temperatures recorded in lower Penobscot Bay during the same months of the year at 40-60 m were

considerably higher, i.e., 3°C west of Islesboro in May 1970[6] and 11°-12°C at various stations in the lower Bay in August 1976[7]. In Penobscot Bay, *P. montagui* were smaller after their first year's growth than in the two North Sea locations (Mistakidis 1957; Allen 1963) but attained approximately the same size by the end of the second year. Males in the Thames estuary measured 10 mm average CL by November of their first year, and in Northumberland (at 40-60 m depth) they averaged 9.5 mm CL by October; transitionals reached 12.5 mm CL by November of their second year in both locations as compared with 11-13.5 mm CL males of the same age in Penobscot Bay (Fig. 3A), while females in Northumberland reached 14.8 mm CL by November of year 2 as compared with 13-15 mm CL at the same age in Penobscot Bay (Fig. 3C). One-year-old females in Northumberland averaged 10.8 mm CL in October.

Allen's (1963) explanation for this difference between male and female lengths-at-age was that shrimp which mature as females in their first year do so 3-4 wk after males of the same age-group; since growth virtually ceases in the fall and winter, the difference in length attained by the females in the first year is maintained into the third year of life. In Penobscot Bay, on the other hand, very few females mature in their first year; however, if males mature in their first year (this was not determined) and stop growing in the fall before the females, Allen's explanation might apply. It seems more likely that sex transition is a function of size, not age, and that the faster growing 0 age-group shrimp complete sex transition in their first year. Another possible explanation for the difference in size of females which change sex in their second and third years is that there may be two distinct periods of larval production and/or survival. Length-frequency data collected at two different periods during the winter (Fig. 3C, G) did suggest that older females may have spawned earlier than younger females. A 5-yr study of *P. borealis* in the Sheepscot River of Maine[8] failed, however, to reveal any consistent bimodality in larval production during February-April even though at least two age-groups of ovigerous females are commonly observed in commercial catch samples[9]. We contend, therefore, that the most plausible explanation for differences in the sizes of shrimp which become females in their second and third years is a difference in growth rates, especially since a similar difference in size was observed between male and female *D. leptocerus* in which sex remains fixed throughout life.

Pandalus montagui which either began life as females or became females early in their first year were smaller than their male counterparts by November-December of their first year (Fig. 3A, B). It therefore seems probable that the smaller Stage I (6.5-8.5 mm CL) females captured in late January (Fig. 3F) did not grow as rapidly as the larger females in the same age-group which apparently completed sex transition in late December and early January or as shrimp which remained as males for the entire year (Fig. 3D). These differences in length-at-age between 0 age-group males and both groups of females were also evident in late March (Fig. 3H, J). The accelerated growth rate of 0 age-group individuals which changed sex during their first year contrasts with the reported faster growth of *P. montagui* in the North Sea and at Grand-Rivière which began life as females (Allen 1963; Couture and Trudel 1969b).

Winter Migration

During November-December 1980, younger male and non-ovigerous female *D. leptocerus* were predominant in shallow water in area 1 (Figs. 4A, 5A) while the older age group predominated in deeper water (Figs. 4B, C, 5B, C). By late January, the older females were no longer being caught, and the older males had disappeared completely from depths < 50 m (Fig. 4D, E), but accounted for about 50% of the males collected in deep water in area 3 (Fig. 4F). There were older males in areas 2 and 3 (moderate and deep water) in March (Fig. 4G, H). These results suggested that older male shrimp migrated down the Bay into deeper water as the winter progressed and as bottom water temperatures dropped from about 8°C in early December to 1°C in late February and early March in the upper Bay.[10] Their disappearance from the catches,

[6]Muirhead, C. R., and J. H. Wartha. 1971. Temperature-salinity observations, Penobscot Bay, Maine, 1970. Oper. Data Rep. NOS DR-13, U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Off. Mar. Surv. Maps, Oceanogr. Div., Descr. Oceanogr. Sect., Rockville, MD.

[7]Central Maine Power Co., unpublished data, courtesy Richard Birge, Environmental Studies Department, CMP, August, ME.

[8]Stickney, A. P. Environmental physiology of northern shrimp, *Pandalus borealis*. Maine Dep. Mar. Resour., West Boothbay Harbor, ME, Annu. Rep. 1981-82, 15 p.

[9]Diodati, P., S. H. Clark, D. McInnes, R. Tichko, and D. Sampson. 1983. Gulf of Maine northern shrimp stock status -1983. Northern Shrimp Technical Committee, November 1983, 9 p.

[10]Birge, R. P. 1982. Surface and bottom water temperatures, upper Penobscot Bay, Maine, March 1975 - December 1981. Central Maine Power Co., Environmental Studies Department, Report SI-82-3, 45 p.
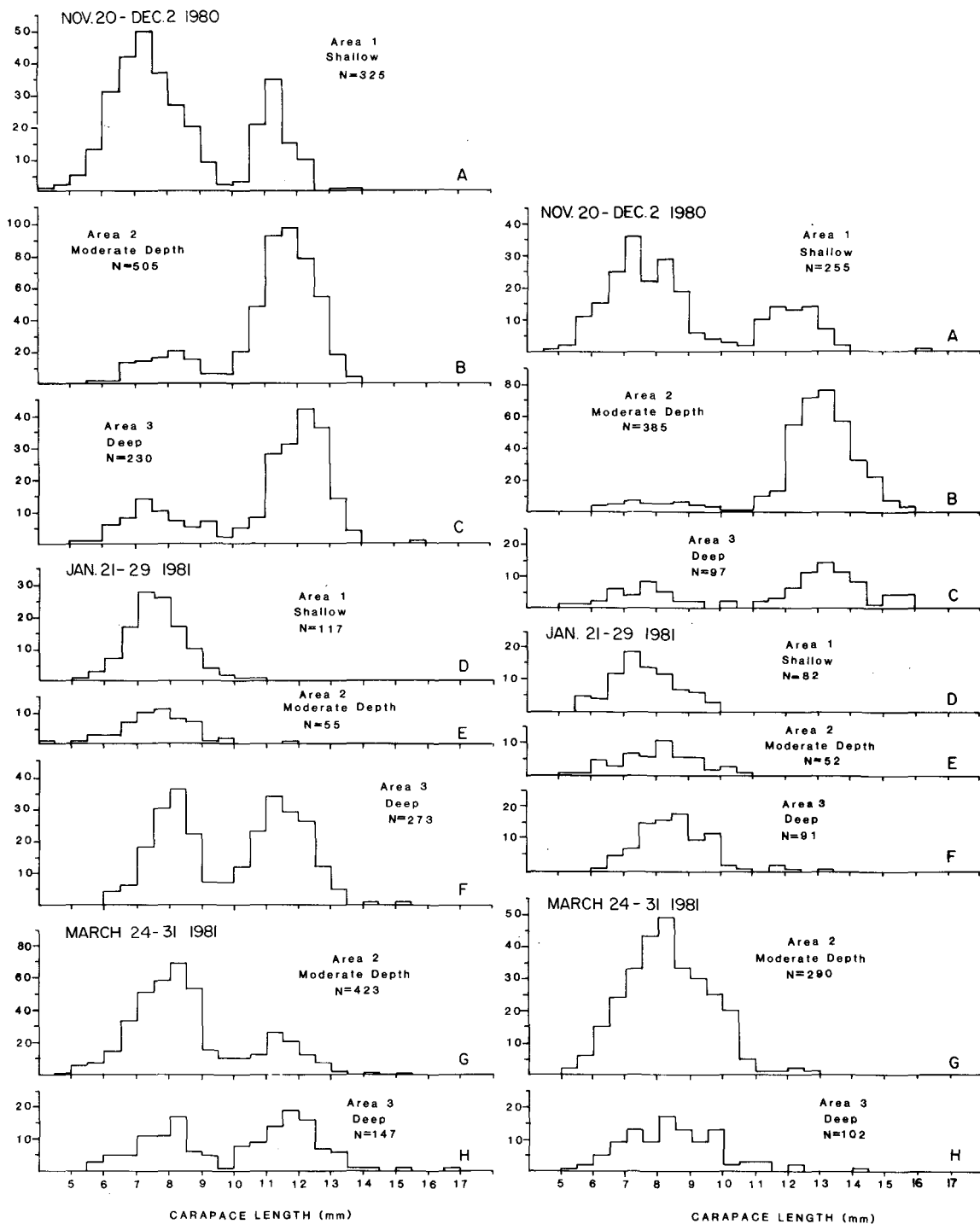
FIGURE 4.—Male *Dichelopandalus leptocerus* numerical length-frequency distributions by area and depth range.

however, may still have been a result of mortality rather than migration. The depth-area length-frequency data also revealed that slightly larger shrimp of both sexes and age-groups were captured in deeper water further down the Bay, suggesting that larger individuals are more likely to migrate than smaller ones.

Older male *P. montagui* also migrated down the Bay into deeper water during the winter: older age-1 males were more abundant than younger 0 age-group males in areas 2 and 3 (moderate and deep water, respectively) in November-December 1980 (Fig. 6A, B, C) and by late January nearly all the older males were in deep water in area 3 (Fig. 6D, E, F), but were not as abundant as the younger males in deep water in area 4 (Fig. 6G). There was no clear evidence that the larger males in either age-group
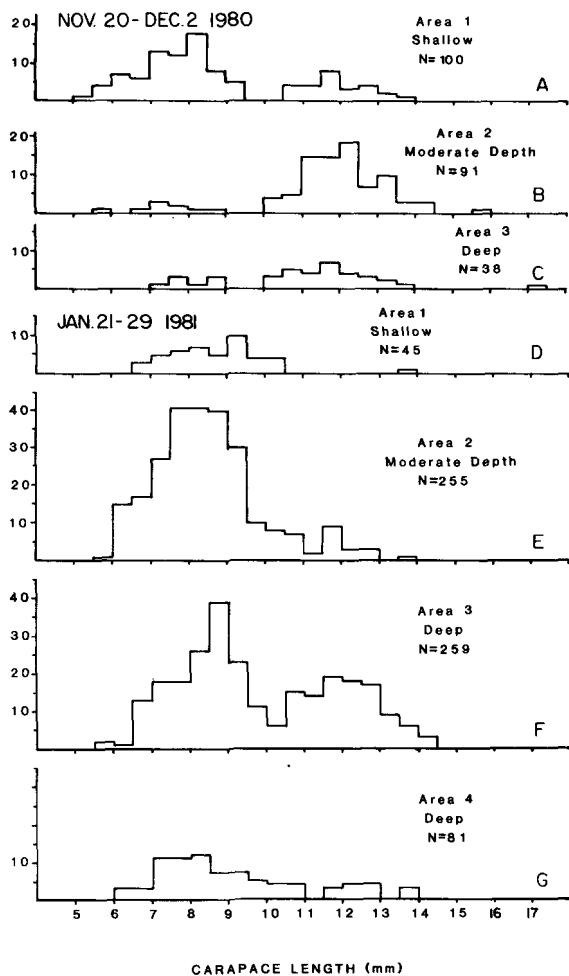
FIGURE 6.—Male *Pandalus montagui* numerical length-frequency distributions by area and depth range.

were more frequent in deeper water and not enough females were collected during any single sampling period to permit an analysis of differential distribution of different age-groups by depth.

Allen (1963) reported an offshore migration of age-1 males to deeper water in the spring and summer in Northumberland waters; Couture and Trudel (1969a) observed the same phenomenon in Grand-Rivière in the summer as the temperature exceeded 6°C and reported that it was triggered by the onset of maturity; earlier maturing males migrated sooner than later maturing males, indicating that migration was a function of size, not age. Mistakidis (1957) and Allen (1963) both reported an offshore migration of *P. montagui* females in the fall; Allen, however, reported that the smaller females stay behind to spawn in shallow water and that there was no "massive" return migration in the spring whereas Mistakidis reported a general offshore fall migration of females and a return migration in the spring. Allen (1963) reported that females in Northumberland which survived to spawn a third time were only found in depths > 100 m.

CONCLUSIONS

This study of the life histories of *Pandalus montagui* and *Dichelopandalus leptocerus* in Penobscot Bay has revealed some notable differences in reproductive characteristics and (apparently) in longevity between the two species. On the other hand, growth rates and migratory behavior were similar.

Most importantly, *P. montagui* is hermaphroditic; *D. leptocerus* is not. In 1980-81, some transitional *P. montagui* were observed during all five sampling periods, but were most common in the early spring; most individuals change sex at the end of their second year but some do so during their first year and a few may not change sex until their third year. Some individuals apparently begin life as females; 15% of the 0 age-group which recruited to trawl catches at 5-10 mm CL in November-December 1980 were females. Ovigerous *P. montagui* were collected over a longer time period, owing, at least in part, to the presence of more age-groups in the spawning population. Most *D. leptocerus* females spawn during their second year, although a few also spawn in their first year; ovigerous females were collected primarily in late November-early December. *Pandalus montagui* spend 1-2 yr as males; individuals which undergo sex transition in their second year may function as females during their second, third, and fourth years while those which change sex in their third year may only function as females for 2 yr. Judging from the

length-frequency data collected during this study, it is unlikely that very many *P. montagui* survive in the Bay beyond age 4. No *D. leptocerus* females older than age 2 were caught in the Bay although some males remained until their third fall (age, 2 yr and 9 mo). Conclusions concerning longevity were complicated by the fact that larger individuals of both species migrated down the Bay into deeper water as the winter progressed and were not captured and by the difficulty of inferring age from length data for the larger size-groups, particularly for *P. montagui*.

Both species were similar with respect to growth and migratory behavior. Growth decreased with increasing age and was seasonal, i.e., rapid in the spring and summer of the first year and the spring of the second year and negligible in the fall and winter. Males of both species reached 7-9 mm CL at age 1 and 11-13 mm CL at age 2. The data suggested that early (age 1) transitional *P. montagui* also grow considerably more rapidly than the remainder of their age group which undergo sex transition at age 2. The slowest observed growth rate was for *P. montagui* which apparently begin life as females and therefore never undergo sex transition. For *D. leptocerus*, females grow more rapidly than males and differential growth is a "fixed" sexual attribute. For *P. montagui*, the fact that the faster growing individuals change sex a year earlier and therefore function as females for an additional year (assuming that fast- and slow-growing shrimp have identical lifespans) means that more rapid growth and early sex transition increase the reproductive potential of the population, as long as enough males remain in the population to mate with the females. Female maturity is clearly a function of size, not age.

The life cycle of *P. montagui* in Penobscot Bay was quite different in several respects from the life cycles of populations which have been studied in the North Sea and at Grand-Rivière, Quebec. *Pandalus montagui* populations in two locations in the North Sea (Mistakidis 1957; Allen 1963) appeared to grow more rapidly in their first year of life than in Penobscot Bay and were composed of a considerably greater proportion of early maturing females, many of which never functioned as males. Growth over the entire lifespan was considerably more rapid in Penobscot Bay and the North Sea than at Grand-Rivière (Couture and Trudel 1969b), but the relative scarcity of females which do not function first as males and the delay of most sex transition until the third year were common to the Canadian and United States populations. In addition to a difference in the timing of maximum sex transition from age 2 (Penobscot Bay and Grand-Rivière) to age 1 (North Sea), the

seasonal intensity of sex transition was not the same in three of the populations. Most transitionals were observed in March in Penobscot Bay, in June in Northumberland (Allen 1963), and in October at Grand-Rivière (Couture and Trudel 1969b). Eggs were carried by females in both North Sea locations and in Penobscot Bay during the winter (November-March); at Grand-Rivière most ovigerous females were observed in October.

In Penobscot Bay and the North Sea, sex transition tended to follow the end of the breeding season, whereas in Grand-Rivière, maximum sex transition coincided with the time when most females were carrying eggs (unless sex transition was more common later in the fall when no samples were collected), suggesting that there was a 12-mo interval between the appearance of external female characteristics and spawning at Grand-Rivière, and a 6-9 mo interval in Penobscot Bay and Northumberland. More rapid growth rates in the latter two locations would explain the shorter time intervals between sex transition and spawning. The reproductive cycle in Grand-Rivière was seemingly continuous, beginning in July and ending in June (Couture and Trudel 1969b).

Although an offshore migration of larger male *P. montagui* was observed in Penobscot Bay, Grand-Rivière, and Northumberland, this migration occurred in the winter following the end of the spawning season in the Bay and in spring and summer, prior to spawning, in the other two locations. Similar movements of larger females have been noted in both North Sea populations in the fall. Unlike the other migrations, the one observed in Penobscot Bay was not a spawning migration and may instead have been a response of older shrimp to declining winter temperatures in the shallower waters of the upper Bay. The departure of significant numbers of older shrimp from the Bay could certainly affect any conclusions concerning the size or age structure of either population and their estimated maximum lifespans.

ACKNOWLEDGMENTS

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