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NOAA Technical Report NMFS 30

Synopsis of Biological Data on the Pink Shrimp, *Pandalus borealis* Krøyer, 1838

May 1985

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U.S. DEPARTMENT OF COMMERCE
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Sandra E. Shumway, Herbert C. Perkins,
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U.S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, Secretary
National Oceanic and Atmospheric Administration
John V. Byrne, Administrator
National Marine Fisheries Service
William G. Gordon, Assistant Administrator for Fisheries

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*No information available.

Synopsis of Biological Data on the Pink Shrimp, *Pandalus borealis* Krøyer, 1838

SANDRA E. SHUMWAY, HERBERT C. PERKINS, DANIEL F. SCHICK,
and ALDEN P. STICKNEY[1]

ABSTRACT

This synopsis of the literature was designed to summarize the biological and biochemical studies involving *Pandalus borealis* as well as to provide a summary of the literature regarding the fisheries data published before early 1984. Included are many unpublished observations, drawn from studies at the State of Maine Department of Marine Resources Laboratory in West Boothbay Harbor, Maine.

INTRODUCTION

Pandalid shrimp represent an important commercial and ecological group worldwide. The pink shrimp, *Pandalus borealis*, is by far the most abundant and important commercial species in the northeast Atlantic, yet a comprehensive summary of the vast literature is lacking. Indeed, *P. borealis* is conspicuous in its absence in a series of synopses on pandalid species (*P. montagui*, Simpson et al. 1970; *P. platyceros*, Butler 1970; *P. jordani*, Dahlstrom 1970). Two bibliographies have been published, one emphasizing the commercially important species of *Pandalus* (Scrivener and Butler 1971) and the other the relationship between distribution of *P. borealis* and oceanographic parameters (Ippolito et al. 1980) and these were of great benefit in preparing the present work. This paper summarizes the available biological data for the species.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name (from Rathbun, 1904)

Pandalus borealis Krøyer, 1838, Naturh. Tidsskrift. vol. II, p. 254-255; (2)I, 461, 1845; in Gaimard's Voyage en Scandinavie, en Laponie, etc., pl. VI, fig. 2. Stimpson, J. Boston Soc. Nat. Hist., VI, 501 (61), 1857; Ann. Lyc. Nat. Hist. N.Y., X, 128, 1871.—Smith, Trans. Conn. Acad. Arts Sci., V, 86, 1879.—Birula, Ann. Mus. Zool. Acad. Imper. Sci. St. Petersbourg, 1897, p. 420 (16); 1899, p. 22 (3), 28 (9).

1.12 Objective synonomy

Dymas typus Krøyer, 1861
Pandalus borealis typica Retovsky, 1946

1.2 Taxonomy

1.21 Affinities

Suprageneric

Phylum Arthropoda
  Class Crustacea
    Subclass Malacostraca
      Order Decapoda
        Suborder Natantia
          Section Caridea
            Superfamily Pandaloida
              Family Pandalidae

Generic

Genus *Pandalus* Leach 1814
Pandalus (from Holthuis, 1955; Hemming, 1956)
Pandalus (Leach), (1814); Brewster's Edinburgh Encyclopedia, 7:432. Gender masculine. Type species, by monotypy: *Pandalus montagui* (Leach), (1814).

The generic concept as used by Holthuis (1955) has been adopted. The following definition of the genus *Pandalus* is based on his key to the pandalidae.

Carpus of 2nd pereiopods consisting of more than 3 joints. No longitudinal carinae on the carapace except the postrostral crest. Rostrum not movable. Eyes well developed, cornea much wider than eyestalk. Third maxilliped without exopod. Laminar expansion of the inner border of the ischium of the 1st pair of pereiopods wanting or inconspicuous. The first 4 pereiopods with epipods. Arthrobranchs present at the bases of the first 4 pereiopods. Posterior lobe of scaphognathite acutely produced. Upper margin of rostrum with movable spine only.

Specific

Pandalus borealis, Krøyer 1838

Butler (1980) gave the following key to species of *Pandalus*:

1a. Third somite of abdomen in part compressed and carinated, carina forms a more or less well-defined lobe or spine in front of posterior margin .2
1b. Third somite of abdomen not compressed or carinated. . .4

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[1] Department of Marine Resources, West Boothbay Harbor, ME 04575.

2a. Third and fourth somites of abdomen each armed with median spine on posterior margin ....Pink shrimp, *P. borealis*

2b. Third and fourth somites without median spines 3

3a. Rostrum unarmed on distal half of dorsal margin ....Flexed pandalid, *P. goniurus*

3b. Rostrum with spines on distal half ....Smooth pink shrimp, *P. jordani*

4a. Dorsal spines absent behind middle of carapace 5

4b. Dorsal spines present behind middle of carapace 6

5a. Sixth abdominal somite more than twice as long as wide ....Yellow-leg pandalid, *P. tridens*

5b. Sixth abdominal somite less than twice as long as wide ....Prawn shrimp, *P. platyceras*

6a. Dorsal spines 17-21 .....Humpback shrimp, *P. hypsinotus*

6b. Dorsal spines 8-12 7

7a. Antennal scale very narrow, distal half of lamella narrower than spine ....Rough patch shrimp, *P. stenolepis*

7b. Antennal scale of moderate width, distal half of lamella wider than spine ....Coonstripe shrimp, *P. danae*

The following description is from Butler (1980) (see Fig. 1). "Body slender, compressed. Shell thin, surface smooth. Rostrum long, 1.5-2.1 carapace length, arched over eyes, distal half ascending, $\frac{12-16}{6-9}$ dorsal spines, except 1-3 distal, movable, tip bifid. Carapace spines: antennal strong, with supporting carina; pterygostomian [spine] weak. Eye large, cornea well developed. Antennule: peduncle moderately long, second segment about twice length of third; stylocerite short, rounded lobe; both flagella somewhat longer than carapace, inner longer. Antenna: scale longer than telson, moderately broad, lamella exceeds spine slightly; basicerite, upper lateral lobe, lower strong spine; peduncle short; flagellum about body length. Third maxilliped: long, moderately stout; antepenultimate segment with slight lamina; epipod. Pereiopods: I longer than third maxilliped, as stout; ischium with slight lamina; proximal part of merus flattened; distal inside surface of carpus with recess bordered by long setae, adjacent distally a pronounced knob; short terminal pegs; epipod; II chelate; epipod, left longer and more slender, ischium with proximal part flattened, and about 5 faint distal annulations; merus, most of length with annulations; carpus about 58 segments; right ischium and merus, with no apparent annulations; carpus, 25-27 segments; III longer than both sides of II, stouter; ischium, 0 or 1 spine; merus, 6 or 7 and 5 spines; carpus, 2 or 3 spines; propodus, 16-18 spinules, 2 rows; dactylus slender, about 0.34 propodus length, 6 or 7 spines, epipod; IV about as long as III, as slender; ischium, 0 or 1 spine; merus, 6-8 and 3-5 spines; carpus, 2 or 3 spines; propodus, 20-22 spinules, 2 rows; dactylus slender, about 0.3 propodus length, 5 or 6 spines; epipod; V shorter than IV, as slender; ischium, 0 or 1 spine; merus, 6-9 and 1 spine; carpus, 1 or 2 spines; propodus, 20-22 spinules, 2 rows; dactylus slender, about 0.28 propodus length, 5 or 6 spines. Abdomen: third somite with dorsal posterior part compressed and carinated, produced posteriorly as strong median spine or lobe, posterior margin produced as acute lobe with small terminal spine; fourth with strong median posterior spine, pleuron with moderate to weak ventral spine; posterolateral margins of fourth and fifth widely recessed at articular knobs; fifth with weak posterolateral spine; sixth shorter than telson, with weak posteroventral spine; telson narrow, tapering to blunt tip, 6-10 pairs dorsolateral spines; inner uropod slightly shorter than outer, both normally shorter than telson.

Color Fine red dots over entire animal, with translucent background. Darker red due to concentration of red dots on dorsal surface and along ventral margin of carapace, distal part of rostrum, basicerite and peduncle of antenna, antennular peduncle and flagella, dorsal surface of abdomen especially third to sixth somites, proximal part of telson, and uropods. Fifth pereiopod more or less uniformly dark red; red dots sparse on proximal segments of other pereiopods; propodi and dactyli of third and fourth pereiopods dark red.

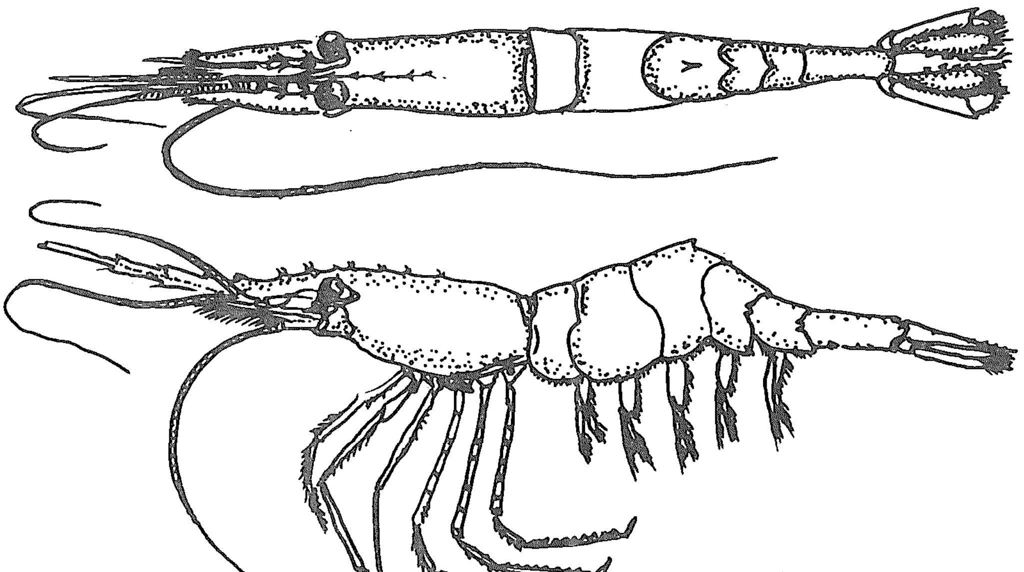

Figure 1.—*Pandalus borealis* Krøyer. Dorsal and lateral views (after Butler 1980).

Distinctions Distinguished by presence of prominent median dorsal spines on third abdominal somite, posterior margin and another at bend of abdomen, median posterior spine on fourth abdominal somite; dorsal spines on distal half of rostrum; in freshly caught specimens, fairly uniform pink to bright red coloration."

Type locality: Sydprøven, Julianehaab, and Fiskenaesset, Greenland (Williams 1984).

1.22 Taxonomic status

The species is distinct from its several congeners and is recognized by all specialists as a valid species.

1.23 Subspecies

Makarov (1935) considered the Bering Sea populations to be of the variety *eous*; species is now considered without varieties.

1.24 Standard common names, vernacular names

FAO names (Holthuis 1980): Northern shrimp (En), Crevette nordique (Fr), Camaron norteno (Sp).

Local names (Holthuis 1980): Dybvannsreke (Norway), Dybhavsreje, Store rde Dybhavsreje, Drammensreje, Norsk reje, Svelviksreje (Denmark), Nordhavsraka (Sweden), Pohjanmeren katkarapu (Finland), Severnyi shrimps WPNMC (U.S.S.R.), Noorse garnaal (Netherlands), Pink shrimp, Deepwater prawn (Great Britain, Canada, U.S.A.), Kampalampi (Iceland), Kingugssvaq, Rafa kingugpak (Greenland), Deep-sea prawn, Great northern prawn, Crevette nordique (Canada), Northern shrimp (U.S.A.), Hokkoku aka ebi, Hokkai ebi (Japan), Chilim (China).

1.3 Morphology

1.31 External morphology

As described above in section 1.21.

1.32 Cytomorphology

Leopoldseder (1934) described the occurrence of four heterochromosomes in the second spermatocytes of *P. borealis*.

1.33 Protein specificity

Johnson et al. (1974) used starch gel electrophoresis to determine population units in five species of pandalid shrimp from Alaska, Washington, and Oregon. They found that all species had similar patterns of protein banding for malate dehydrogenase NAD and NADP, peptidase, tetrazolium oxidase (TO), and glyceraldehyde-3-phosphate dehydrogenase (GAPDH). Esterase patterns were varied, patterns weak and not always repeatable. Lactate dehydrogenase (LDH) patterns were similar in *P. jordani*, *P. borealis*, and *P. goniurus* where *P. hypsinotus* and *Pandalopsis dispar* showed a different pattern from the other three species. Phosphoglucomutase (PGM) was found to be polymorphic in all five species (Fig. 2) and was used in conjunction with LDH and general protein to develop a key for separating the five species (Fig. 3). They suggest that PGM variation may be used in population identification of *P. hypsinotus* (the species with the greatest number of PGM alleles), separation of breeding groups, and as genetic markers in shrimp culturing experiments.

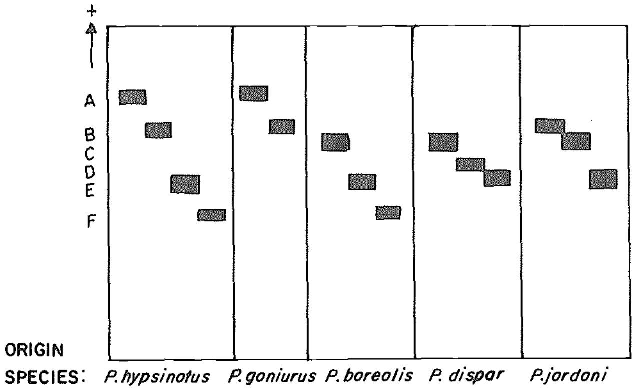

Figure 2.—Diagrammatical representation of the alleles of phosphoglucomutase in five species of pandalid shrimps as shown by the technique of starch gel electrophoresis (from Johnson et al. 1974).

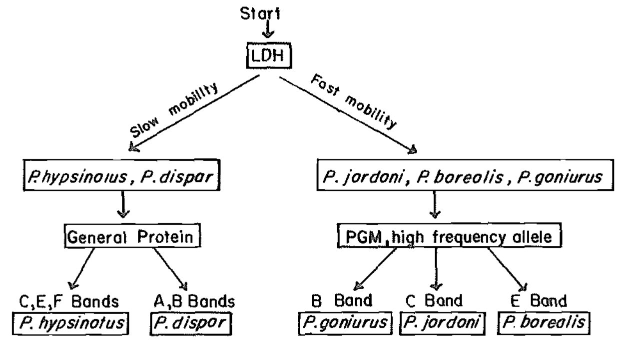

Figure 3.—Key to five species of pandalid shrimp based on three biochemical characters (from Johnson et al. 1974).

Sherburne (unpubl. data) conducted a brief survey of enzyme systems in *P. borealis* using starch gel electrophoresis. He determined the following enzyme systems: hexokinase, phosphoglucomutase, myokinase, aldolase (fructose diphosphate aldolase), aldolase (fructose monophosphate aldolase), lactose dehydrogenase, phosphoglucose isomerase, esterase, glucose-6-phosphate dehydrogenase, ribonuclease, fumarase, and glycerophosphate dehydrogenase. Aldolase and PGM were found to be polymorphic with the particular buffer systems used; hexokinase and myokinase showed some indication of polymorphism, however slight modifications of the buffer systems are necessary to increase resolution.

2 DISTRIBUTION

2.1 Total area

Pandalus borealis is a discontinuous circumboreal species (Fig. 4) common in boreal waters in the following areas (numbers in parentheses indicate FAO geographic classification codes after Rosa 1962): North Atlantic (ANE, ANW): Spitsbergen (Svalbard) (515) and Greenland (250) south to Northumberland, U.K. (532), and Massachusetts, U.S.A. (236); north to Franz Josef Land (716); Norway (514); Iceland (513); North Sea; Barents Sea to North Sea. In the Pacific North (IN) from the Bering Sea, Cape Navarin to Southeast Siberia (710); Chukchi Sea, Point Barrow; Korea (444); Okhotsk Sea; Sea of Japan, Hokkaido, Toyama Bay;

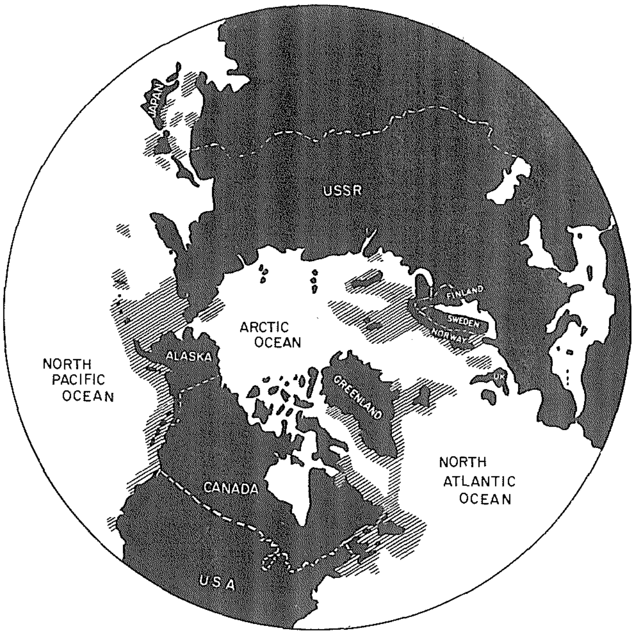

Figure 4.—Distribution of *Pandalus borealis* (hatched areas). Records from section 2.1.

Alaskan coast (220) south to Columbia River (231); eastern Bering Sea and Aleutian Islands (222); Bering Straits to Vrangelye Island (710); Kamchatka Peninsula (710) and southward to Honshu (451); British Columbia (212); stragglers have been reported as far south as San Diego, CA, U.S.A. (232). This distribution ranges from lat. 35°N (Ito 1976) to 82°N (Allen 1959).

References: Allen (1959); Alverson et al. (1960); Berkeley (1930); Blacker (1957); Bryazgin (1967); Butler (1980); FAO (1972); Gaffney (1977a); Gorbunow (1934); Greenwood (1959); Grieg (1925, 1927a, b, 1933); Harry (1964); Haynes and Wigley (1969); Heegaard (1941); Hjort and Ruud (1938); Hofsten (1916); Holthuis (1980); Horsted and Smidt (1956); Hynes (1930); Ito (1976); Ivanov (1967a, b, 1969a); Johnson and Lindner (1934); Kubo (1951, 1956); Kurata (1981); MacGinitie (1955); MacGinitie and MacGinitie (1949); Makarov (1935); Poulsen (1946); Pruter and Harry (1952); Rasmussen (1942, 1953, 1967a); Rathbun (1904, 1929); Retowski (1936); Ronholt (1963); Sigurdsson and Hallgrimsson (1965); Sivertsen (1932); Smidt (1981a, b); Squires (1957, 1966); Stephenson (1935); Vinogradov (1947); Wigley (1960); Williams (1974); Williams and Wigley (1977); Yokoya (1933).

Temperature, substratum, salinity, and depth are all factors contributing to distribution patterns in *P. borealis* populations. The shrimp have been reported in waters with temperatures of −1.6°C (Gorbunow 1934; Ingraham 1981) and ranging upwards to 12°C (Bjork 1913). The most common temperature range is between 0° and 5°C (Apollonio and Dunton 1969; Barr 1970a, b; Bryazgin 1967; Hjort and Ruud 1938; Ingraham 1981; Ivanov 1963, 1967b; Palenichko 1941; Rasmussen 1967c; Smidt 1967; Von Hofsten 1916). Several authors have reported that extended exposure to temperatures below −1°C are deleterious and cause mass mortalities (Horsted and Smidt 1956; Ingraham 1981).

It is generally accepted that *P. borealis* prefers soft mud or sand/silt substrata (Barr 1970a, b; Haynes and Wigley 1969; Hjort and Ruud 1938; Horsted and Smidt 1956; Ivanov 1963, 1967b; Rasmussen 1953; Smidt 1967; Warren and Sheldon 1968) although Berkeley (1930) and Balsiger (1981) have also reported the shrimp from areas with occasional rocks. Further, there is a direct correlation between the abundance of shrimp and the organic content of the bottom sediments (Bigelow and Schroeder 1939; Haynes and Wigley 1969; Hjort and Ruud 1938; Wigley 1960; Wollebaek 1908).

Pandalus borealis is generally considered to be a stenohaline species restricted to waters of fairly high salinity (Allen 1959) although the species has been reported in salinities ranging from 23.4 to 35.7‰ (Abercrombie and Johnson 1941; Allen 1959; Barr 1970a, b; Bryazgin 1967; Butler 1964, 1971; Ivanov 1963; Poulsen 1946).

The depth at which *P. borealis* occurs has been shown to vary with latitude (Rasmussen 1953; Horsted and Smidt 1956); the higher the latitude, the deeper the densest populations. It has also been shown to vary with season (see section 5.31). In general, the shrimp can be found anywhere from 9 to 1,450 m (Balsiger 1981; Haynes and Wigley 1969; Hjort and Ruud 1938; Vinogradov 1947) although they appear to be most common between 50 and 500 m (Allen 1959; Bigelow and Schroeder 1939; Bryazgin 1967; Hjort and Ruud 1938; Ito 1976; Ivanov 1967b; Jensen 1967; Smidt 1967; and Squires 1968).

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

Female *P. borealis* carry their fertilized eggs on their pleopods from the time of extrusion until hatching and release of the larvae. This period of time varies with temperature and ranges from 4.5 mo in Northumberland waters to 9-10 mo in Spitsbergen waters (Fig. 5). Harry (1964) referred to spawning in late September and hatching in March and April for *P. borealis* in the Gulf of Alaska and the Kodiak area.

The apparent migration of females in certain areas to shallower water to release their larvae creates a differential distribution of larvae and juveniles from the adults (Apollonio and Dunton 1969; Berkeley 1930; Haynes and Wigley 1969; Hjort and Ruud 1938; and Horsted and Smidt 1956).

The larvae of *P. borealis* are pelagic and are exposed to currents that affect their distribution upon settling. Horsted and Smidt (1956) stated that planktonic larval influx into Disko Bay and many fjords in west Greenland is critical to the population of *P.*

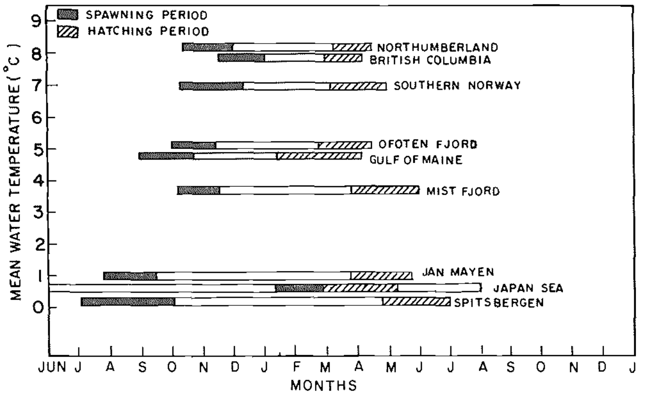

Figure 5.—Comparison of ovigerous periods, breeding season, and hatching period from various shrimp populations (from Allen 1959; Haynes and Wigley 1969; Ito 1976.)

borealis in those areas. Ivanov (1969b) believed circular current patterns in the Gulf of Alaska and in the Bering Sea trap larvae and this allows the repopulation of certain beds of *P. borealis*. Larval *P. borealis* are released in the spring in shallow inshore areas in the Gulf of Maine and are presumed to remain inshore through their juvenile stages (Apollonio and Dunton 1969; Haynes and Wigley 1969; Rinaldo 1973; Schick 1981, 1983). However, Schick and Sampson (1983) found numerous juveniles in offshore summer trawls in the Gulf of Maine in 1979-82 but not prior to 1979 nor in 1983. Berkeley (1930) observed that juveniles were in shallower water (46-64 m) and separate from the stock of adults. Horsted and Smidt (1956) reported similar observations off west Greenland as did Hjort and Ruud (1938) off Norway with the juveniles joining the adult stock near the end of their first year.

2.22 Adults

Within bounds described by temperature, salinity, and depth tolerances, adult *P. borealis* are distributed differentially by size, age, sex, season, and over broader time frames in many populations. Distribution differences occur due to horizontal and vertical movement and due to a tendency to segregate by size in a mixed population. Annual differences in distribution of adults occur with changes in abundance. During years of great abundance, not only is the shrimp density greater but also the total area of distribution can be greatly increased. The tendency for *P. borealis* to segregate on shrimp beds in a patch distribution by size classes has been observed by Ivanov (1964a) near the Pribilof Islands and in the western Gulf of Alaska, by Horsted and Smidt (1956) off west Greenland, by Allen (1959) off Northumberland, and by E. E. Dunton[2] in the Gulf of Maine, while Hjort and Ruud (1938) found evenly mixed year classes in Norwegian waters.

Seasonal distributional changes occur primarily due to migratory impulses expressed by various sex/age classes. Carlsson and Smidt (1978) found changes in the distribution of age classes in Disko Bay, west Greenland, likely caused by warm bottom water intrusion bringing adults into the bay. Migration of berried females into shallower water to release their larvae has been observed off Norway by Wollebaek (1908) and Hjort and Ruud (1938), off Korea by Kim (1966), in the Gulf of Maine (Figs. 6, 7) by Scattergood (1952), Apollonio and Dunton (1969), and Haynes and Wigley (1969), and in west Greenland by Horsted and Smidt (1956). Berkeley (1930) noted that larvae and juveniles were found inshore and shallower than the adults indicating a possible spawning migration inshore. Ippolito (1980) found no evidence of migration in four bays of Kodiak Island, AK. Juveniles in the Gulf of Maine remain inshore where they are exposed to greater temperature range than the offshore population. As they mature into males they migrate offshore possibly reflecting a decrease in thermal tolerance according to Apollonio and Dunton (1969). However, Haynes and Wigley (1969) pointed out that shrimp in the Gulf of Maine exist within the temperature range for *P. borealis* established by Allen (1959).

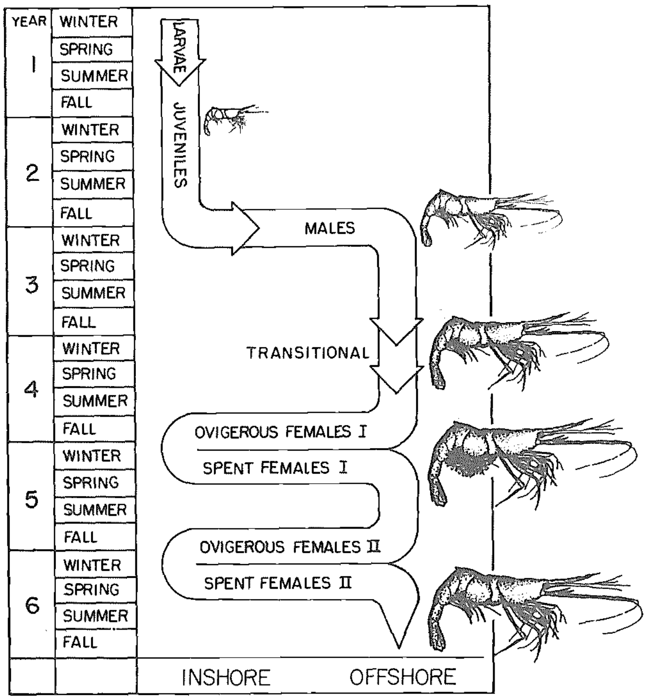

Figure 6.—Schematic diagram of the life cycle of *Pandalus borealis* in the Gulf of Maine (Stickney and Perkins unpubl. data).

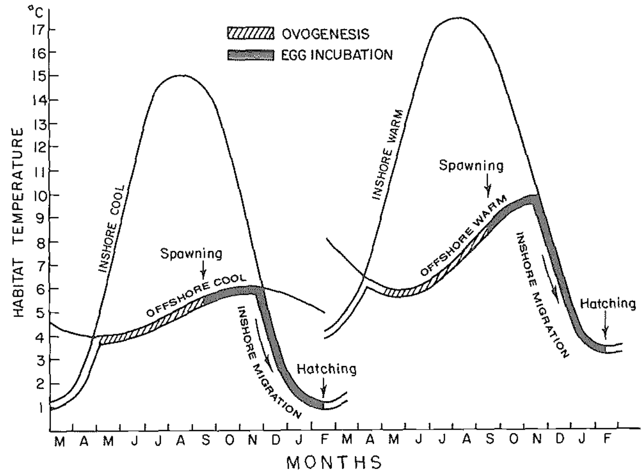

Figure 7.—Idealized representation of seasonal temperature cycles, inshore and offshore, for a hypothetical cold year (left) and a hypothetical warm year (right) (from Stickney 1981).

Diurnal vertical migration of *P. borealis* has been indicated through reduced trawl catches at night in the Barents Sea (Bryazgin 1967), in the Gulf of Alaska (Gaffney 1977a), off Norway (Hjort and Ruud 1938; Wollebaek 1903), off west Greenland (Horsted and Smidt 1956), and by others (Blacker 1957; Rathjen and Fahlen 1962). Work carried out in the Gulf of Alaska by Barr (1970a) determined the extent of migration by the use of surface to bottom pot-fishing techniques. Barr and McBride (1967) found that shrimp moved off the bottom in the early evening and remained in the entire water column until early morning (Fig. 8). Apollonio and Dunton (1969) confirmed vertical migratory behavior in similar experiments in the Gulf of Maine but found the extent of vertical movement limited by a thermocline. Ovigerous females do not migrate vertically apparently due to a decreased ability to swim (Apollonio and Dunton 1969; Haynes and Wigley 1969; Jones and Parsons 1978). Some differences are

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[2] E. E. Dunton, Department of Marine Resources, West Boothbay Harbor, ME 04575, pers. commun. November 1983.

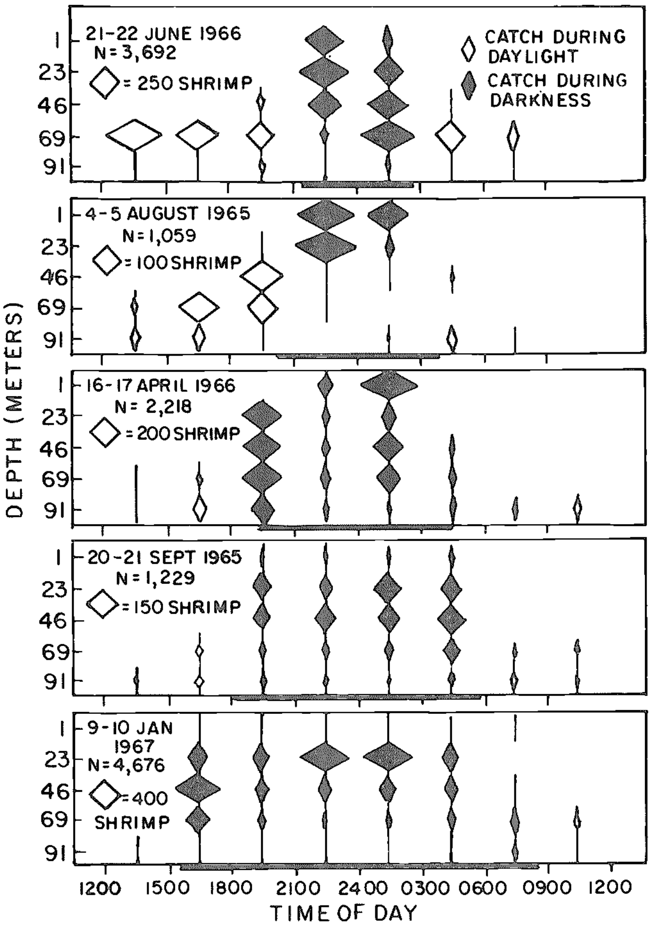

Figure 8.—Total catches of *Pandalus borealis*, by time and depth, taken by surface-to-bottom fishing of two strings of pots in Kachemak Bay, AK. Time between sunset and sunrise is indicated by heavy black line along horizontal axis. Sampling periods are arranged in order of increasing length of night (from Barr 1970a).

evident as Barr (1970a) found that smaller shrimp migrated further up in the water column off Alaska while Carlsson (1979) reported that larger shrimp were participating in the migration to a greater extent than smaller shrimp off west Greenland.

2.3 Determinants of distribution changes

Ecological determinants of the distribution of *P. borealis* include substratum, currents, depth, light, salinity, and temperature.

Most researchers report a close relationship of *P. borealis* with soft substrate and high organic content (see section 2.1). The range of depths, salinities, and temperatures within which *P. borealis* is found has been reviewed in section 2.1. Changes in any of these determinants will affect the population of *P. borealis*. Of these, temperature has been correlated most closely with changes in abundance of *P. borealis* (Dow 1963, 1964, 1966, 1967a, b, 1973, 1977b, 1981). Horsted and Smidt (1956), Ingraham (1981), and Smidt (1969) referred to a mass mortality of *P. borealis* in 1948-49 in a west Greenland fjord when water temperature dropped to −1.6°C. Apollonio and Dunton (1969) showed no vertical migration through the thermocline in the Gulf of Maine. Dow (1964) has correlated optimum temperatures by month for shrimp landings 2 yr later (see section 4.42, Table 30). Ivanov (1969a) has correlated the success of shrimp year classes near the Pribilof Islands with the temperature of the first winter for each year class. Squires (1970) found an increase in the percentage of males as bottom temperatures dropped below 1.0°C off Newfoundland (Table 1). Rasmussen (1969) observed changes in hermaphroditism between southern and northern populations of *P. borealis* in Norwegian waters. Ivanov (1964b) observed a decrease or lack of females on the colder shelf waters bordering beds of *P. borealis* in the Bering Sea. Horsted and Smidt (1956) observed that deep currents affect the distribution of *P. borealis* in west Greenland fjords and in Disko Bay. Ivanov (1964a) has correlated the densities of concentrations of shrimp near the Pribilof Islands with areas of mixing of different water masses and with circular current regimes that trap larvae. Klimenkov et al. (1978) related shrimp concentrations off west Greenland with current structure and Carlsson and Smidt (1978) discussed the distribution of shrimp larvae by currents in the same area. Ippolito (1980) discussed the possible role of the Alaska Stream in the distribution of shrimp stocks off Kodiak Island.

Barr (1970a) demonstrated that light affects shrimp in their diel vertical migration in Alaska (Fig. 8). Apollonio and Dunton (1969) also demonstrated negative phototaxis of *P. borealis* adults. Ivanov (1967b) referred to Thomsen's demonstration of positive phototropism in larvae of *P. borealis* and postulated a similar reaction by larval *P. borealis*.

Behavioristic determinants of distributional changes of shrimp are spawning migrations and feeding activities. Migrations of ovigerous females to release their larvae in shoal water in the Gulf of Maine produce a separation of year classes that has been thoroughly discussed by Apollonio and Dunton (1969). Haynes and Wigley (1969), Rinaldo (1973), and Schick et al. (1981) also referred to migration in the Gulf of Maine. Wollebaek (1908) referred to migration in Norwegian fjords as do Horsted and Smidt (1956) for west Greenland waters and Kim (1966) for Korean waters. Vertical migration at night has been shown by Barr (1970a) and Apollonio and Dunton (1969) to separate year classes during seasons when females are ovigerous as the females do not rise in the water.

Table 1.—Ratio of males to females in random subsamples from catches of *Pandalus borealis* by the *Fortune Breeze* (1957-58) at different bottom water temperatures (from Squires 1970).

Temperatures (°C)	Number of hauls	M/F
−1.5 to −1.1	7	8.0
−1.0 to −0.5	[1]7	13.5
−0.4 to 0.0	4	6.7
0.1 to 0.5	2	(males only)
0.6 to 1.0	[1]8	18.5
1.1 to 1.5	2	17.6
1.6 to 2.0		
2.1 to 2.5	1	(males only)
2.6 to 3.0	1	8.1
3.1 to 3.5		
3.6 to 4.0	1	2.8
4.1 to 4.5	7	0.7
4.6 to 5.0	6	0.6
5.1 to 5.5	12	1.1
5.6 to 6.0	10	1.4
6.1 to 6.5	3	1.3

[1] Three hauls had males only.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Hermaphroditism

Berkeley (1930) first noted that *P. borealis* is a protandric hermaphrodite, i.e., each individual matures and functions first as a male, passes through a transitional or intersexual phase, and becomes a female. While this is the normal sequence of events, several authors have reported early maturing females in the southern portions of the range. The following categories of shrimp development are given by Haynes and Wigley (1969): 1) two classes of males, immature and mature; 2) four transitional stages, each stage represented by a molt (see Table 4); 3) three classes of females, primary, in which male characteristics never appear; secondary in which potentiality is repressed soon after male characteristics appear; and hermaphroditic in which male potentialities are repressed after the shrimp function as males. They reported examples of all of the above classes in the Gulf of Maine although Apollonio and Dunton (1969) found no primary females. Allen (1959) and Jagersten (1936) reported incidences of primary females and secondary development had been reported by Haynes and Wigley (1969), Rasmussen (1953), and Butler (1964) among others.

Sex reversal in *P. borealis* has been used as a model for studying the benefits of protandry by several authors. Ghiselin (1969, 1974) and Warner (1975) proposed a size-advantage model to explain the survival value of protandry. The model as given by Warner (1975) states that "... an individual reproduces most efficiently as a member of one sex... when it gets older or larger." *Pandalus borealis* is an example of a species where the small males produce energetically less demanding sperm while the larger females produce the metabolically demanding eggs.

Carpenter (1978) believed that protandry is a neutral attribute amongst the Decapoda with no adaptive value in that it is neither useful nor harmful and argued that in some situations, e.g., cataclysmic disruption of habitat, it could be markedly maladaptive.

Sexual dimorphism

The sexes of *P. borealis* can easily be distinguished by certain external structures on the 1st and 2nd pleopods (Fig. 9). The changes in these structures have been studied in detail by Berreur-Bonnenfant and Charniaux-Cotton (1965), Allen (1959), and Rasmussen (1953) and are shown in Figure 10.

3.12 Maturity

Several factors are known to affect sex reversal and consequently the age and size at maturity. Rasmussen (1953) and Fox (1972) have indicated that time of sex reversal is related to individual size and there is considerable geographic variation in age at sex reversal (see Tables 2, 3). Apollonio and Dunton (1969) argued that temperature plays a significant role in determining the time of sex reversal. In general, age at maturity increases with decreasing temperature (Fig. 11). In addition, Rasmussen (1967a) showed that cycles of growth and maturity vary not only from locality to locality but from brood to brood in the same locality.

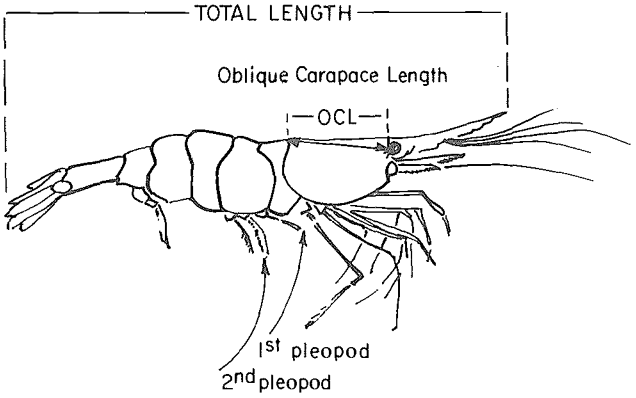

Figure 9.—Method of measuring the carapace of *Pandalus borealis* and location of the first and second pleopods.

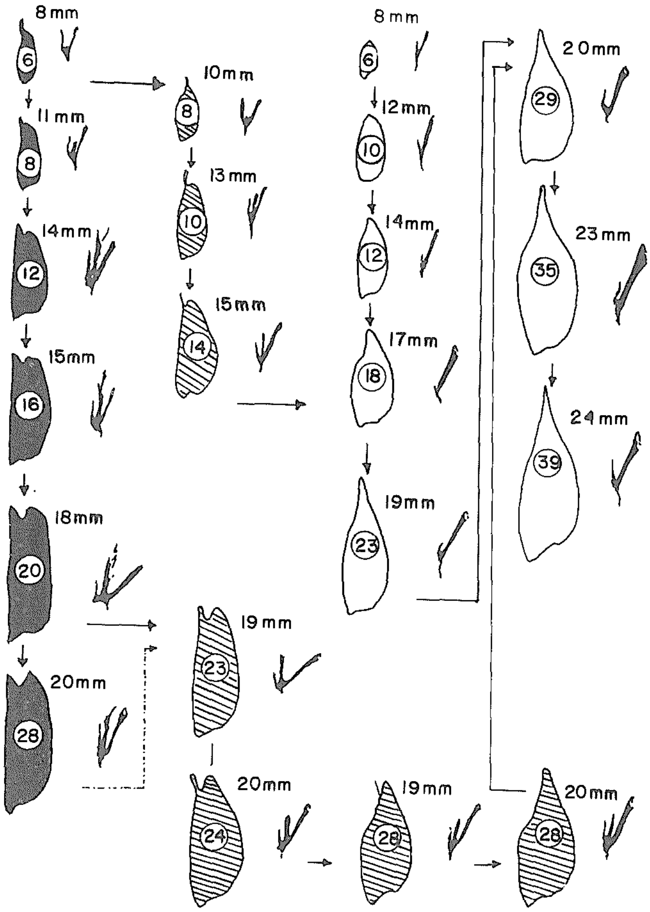

Figure 10.—Changes in form with increasing age of the endopodite of the first pleopod and the corresponding appendix interna and appendix masculina of the second pleopod of *Pandalus borealis* from the Northumberland population. Age in months is given in the ring in each endopodite and the carapace length (mm) above each figure. Male endopodite, black; transitional, cross-hatched; female, outlined. Arrows indicate sequence (from Allen 1959).

Based on the data of Jensen (1965, 1967), Charnov (1981) suggested that the predicted age of sex reversal is most sensitive to the adult mortality rate, i.e., the higher adult death rates select for a shorter time spent as a male, and not to growth rates. He attributes the build up of the shrimp fishery (which tends to concentrate on female shrimp) to the changes in size at sex reversal reported by

Table 2.—Size, development stage, and approximate age of *Pandalus borealis* from various locations.

Size (mm)	Approximate age (yr)	Stage of development	Location	Reference
OCL 13-15	1.5	low %♂: mostly immatures	Barents Sea	Bryazgin (1967)
18-19	2.5	♂: transitionals		
23-24	3.5	⚥: first spawners		
>27	4.5	♀; first and later spawners		
CL 11.0	0.67	♂	British Columbia	Butler (1964)
12.8	1.0	♂		
14.3	1.17	♂: (Θ)		
16.1	1.58	♂; (♀)		
17.8	2.0	⚥; (♀)		
20.6	2.5	♀		
22.1	3.17	♀		
OCL 15	2	—	Japan Sea	Ito (1976)
20	3	—		
25	4	—		
OCL 12-13	1.5	immature	Bering Sea	Ivanov (1969a)
18-19	2.5	⚥; some immature		
22	3.5	♂		
24-25	4.5	♂		
	5.0	⚥		
27	5.5	first spawners		
	6.5	sterile ♀		
TL 39	1	immature	Norway	Rasmussen (1953)
65	2	immature; ♂		
87	3	♂		
104	4	⚥		
119	5	♀ first spawners		
122	6	spent		
140	7	♀ second spawners		
CL 12.9 (approx.)	1.58		Iceland	Skuladottir (1981a)
14.1	1.83			
17.1	2.58			
17.6	2.83			
21.1	3.58			
21	3.83			
22.9	4.58			
23	4.83			

Jensen. Warner (1975) also pointed out that, on a broad geographic scale, the amount of time spent in the male phase was consistent with sex change theory and this conclusion was supported by analyses by Charnov (1979).

3.13 Mating

The available information on mating behavior in *P. borealis* is scant and only incidental to other studies. Apollonio and Dunton (1969) stated that mating takes place offshore during the summer. Butler (1970) assumed the process in *P. platyceros* to be similar to that described by Needler (1937) for *P. danae* and the process is no doubt similar in *P. borealis*. Butler (1970) gave the following account.

"The female generally moults at night and apparently mating and oviposition occur within 36 h after this moult. The male locates the nubile female through a kinesis reminiscent to that when the animal is near food. The first action of the male is an attempt to run up the back of the female, but he may be shaken off by the larger female. When the male succeeds in holding the female he assumes a position with the anterior part of his abdomen under the posterior part of her cephalothorax; sometimes the female rolls over and the two lie side by side. Copulation generally takes a minute or less, leaving the female with a loose mass of spermatozoa between the bases of the last 2 pairs of pereiopods. Oviposition is carried out while the female is on the bottom, resting on the dactyli of the 3rd pereiopods and on the telson. The 4th and 5th pairs of pereiopods are bent under the body and are kept active in an 'elbowing' motion. The pleopods move gently and continuously, and the eggs pass from the oviducts in a steady stream between the pereiopods to the abdomen, becoming attached to the anterior pleopods first. Oviposition lasts about half an hour, but afterwards, the female may remain in position for the same period before moving about normally."

The only published information on mating by *P. borealis* is that of Carlisle (1959b). He described the mating process as follows: once the male has touched an attractive female (a female which has just undergone the molt of copulation) with his antenna, he begins to swim rapidly in circles, "then with quick sharp motions, once he has found the female again, palpates her all over with his chelae. Copulation normally follows, but if several males are in a tank there may be some fighting."

Table 3.—Composition of major sex stages during the spawning season for 10 populations of northern shrimp. [Numbers in parentheses are total lengths (mm) of shrimp.][1]

Age and locality	Percentage of immature males	Percentage of mature males	Percentage of mature females
1.5 yr			
Gulf of Maine	—	>99.9 (83-111)	<0.1 (104)
British Columbia	—	53 (73-111)	47 (99-120)
Northumberland	—	63.5 (76-90)	36.5 (81-96)
S. Norway	—	82-99.5 (80-94)	0.5-18 (90-101)
Ofoten Fjord	0-0.2 (58)	99.8-100 (58-85)	—
W. Greenland and Jan Mayen	100 (49)	—	—
Spitsbergen	100 (40)	—	—
Gulf of Alaska[2]	100 (63)	—	—
Bering Sea[2]	100 (70)	—	—
Iceland[3]	—	100 (67)	—
2.5 yr			
Gulf of Maine	—	70-82 (112-141)	18-30 (112-141)
British Columbia	—	—	100 (>140)
Northumberland	—	—	100 (100-126)
S. Norway	—	0-78.5 (96-111)	21.5-100 (120-130)
Ofoten Fjord	—	16-88.5 (92)	11.5-84 (100-103)
W. Greenland and Jan Mayen	100 (69)	—	—
Spitsbergen	86-99 (64)	1-14 (78)	—
Gulf of Alaska	100 (89)	—	—
Bering Sea	15 (83)	85 (89)	—
Iceland	—	100 (77)	—
3.5 yr			
Gulf of Maine	—	—	100 (124-164)
British Columbia	—	—	100 (>140)
S. Norway	—	—	100 (130-140)
Ofoten Fjord	—	—	100 (122-143)
W. Greenland and Jan Mayen	—	100 (94)	—
Spitsbergen	—	100 (87)	—
Gulf of Alaska	96 (100)	1 (108)	3 (105)
Bering Sea	—	99.2 (102)	—
Iceland	—	20 (89)	80 (89)
4.5 yr			
Gulf of Maine	—	—	100 (160-182)
S. Norway	—	—	100 (150-159)
Ofoten Fjord	—	—	[4]
W. Greenland and Jan Mayen	—	71 (115)	29 (126)
Spitsbergen	—	100 (104)	—
Gulf of Alaska	—	2 (109)	90 (113)
Bering Sea	—	96.8 (111)	3.2 (116)
Iceland	—	—	100 (98)
5.5 yr			
W. Greenland and Jan Mayen	—	—	100 (139)
Spitsbergen	—	—	100 (118)
Gulf of Alaska	—	—	100 (120)
Bering Sea	—	—	100 (125)
Iceland	—	—	100 (106)
6.5 yr			
Spitsbergen	—	—	100 (121)
Bering Sea	—	—	100 (135)
Iceland	—	—	100 (113)
7.5 yr			
Spitsbergen	—	—	100 (140)
Bering Sea	—	—	100 (145)
Iceland	—	—	100 (118)
8.5 yr			
Spitsbergen	—	—	100 [4](>140)
Iceland	—	—	100 (122)
9.5 yr			
Spitsbergen	—	—	100 [4](>140)
Iceland	—	—	100 (127)

[1] First seven populations are from Haynes and Wigley (1969).

[2] Gulf of Alaska and Bering Sea are from Ivanov (1969b) with some interpolation of his data.

[3] The lengths at age are from Skuladottir (1979) using a carapace length to total length conversion of 4.8, and the sex at length is from Sigurdsson and Hallgrimsson (1965) whose length and age agree fairly closely with Skuladottir for the first 4.5 yr.

[4] Very few specimens.

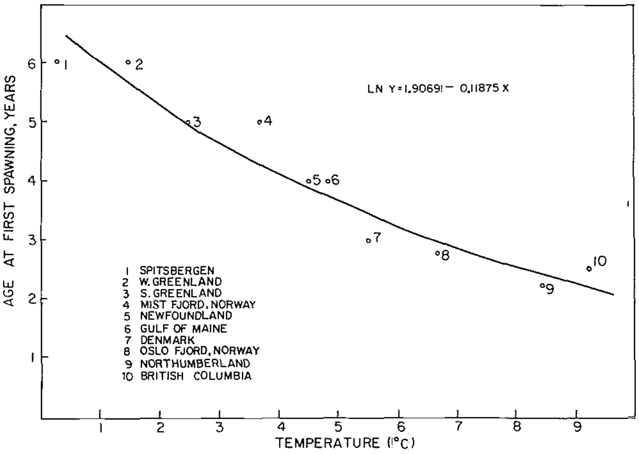

Figure 11.—The relation between the average annual bottom temperatures and the ages of the first female maturity of *Pandalus borealis* throughout its geographical range (from Apollonio and Dunton 1969).

3.14 Fertilization

Fertilization is external (see section 3.13) and occurs just prior to the time of egg laying.

3.15 Gonads

Descriptions of the gonads of *P. borealis* have been given by several authors (Wollebaek 1903; Berkeley 1930; Leopoldseder 1934; Jagersten 1936; Charniaux-Cotton 1963; Berreur-Bonnenfant and Charniaux-Cotton 1965). The gonads consist of an elongate pair of tubular structures joined by a bridge about a third of the distance from the anterior end (Fig. 12). The vas deferens and oviduct join the gonad midlaterally and the oviduct is anterior to the vas deferens (Berkeley 1930). Figure 13 shows a detailed figure of the vas deferens gland after Carlisle (1959a) while Figure 14 shows a detailed diagram of the gonad after Berreur-Bonnenfant and Charniaux-Cotton (1965).

Allen (1959) took oocyte measurements from transverse sections of gonads and compared them with the age of the individual

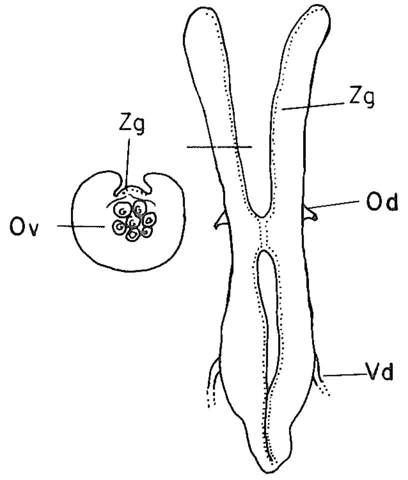

Figure 12.—The gonad of *Pandalus borealis* (male phase). Zg: germinative zone; Od: oviduct; Vd: vas deferens; Ov: ovocyte (after Berreur-Bonnenfant and Charniaux-Cotton 1965).

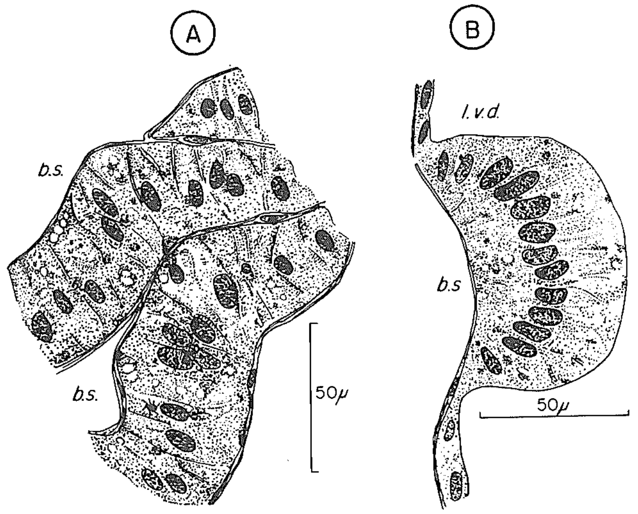

Figure 13.—A) Part of the massive portion of the vas deferens gland. Note the fibrous sheath; b.s.: blood sinus. B) A transverse section of the strand of the vas deferens, with a portion of the squamous epithelium of the duct. Note the continuous fibrous sheath over the outer side of both duct and strand; l.v.d.: lumen of the vas deferens (after Carlisle 1959a).

shrimp (Fig. 15). He also gives a detailed analysis of oocyte development in primary females, hermaphroditic females, and secondary females. Table 4 discusses the changes in ovary development during sexual development.

3.16 Spawning

Females spawn once a year. Extrusion of eggs starts in late summer to early fall and the ovigerous period lasts until spring; however, the exact time of hatching is directly related to water temperature, the warmer the water, the earlier the hatching (Rasmussen 1953; Couture 1970) (Fig. 5). The eggs are about 1 mm wide and 2 mm long, oval, opaque, and quite blue. The opacity and blue color (yolk) gradually decrease as the embryo consumes the yolk material.

Stickney and Perkins (1980) demonstrated that there is a direct relationship between the summer water temperature and the duration of ovogenesis and time of egg extrusion. They found a tendency for longer periods of ovogenesis and later extrusion at lower temperatures according to the equation: $\log_{10}Y = 2.12 - 0.52 \log_{10}X$ where Y is the number of days until extrusion and X is the temperature in degrees Celsius. They used this laboratory calculation to extrapolate a relationship for the entire period of ovogenesis assuming the date of initiation of ovogenesis and an estimated full term of 164 d at 5°C. They gave the following equation for the full term of ovogenesis: $\log_{10}Y = 2.593 - 0.54 \log_{10}X$.

Using these equations it was estimated that a 2°C difference in average summer temperature could alter the duration of ovogenesis by 36 d (Fig. 16).

3.17 Fecundity

Several authors have reported on the fecundity of this species from various areas (Allen 1959; Apollonio and Dunton 1969;

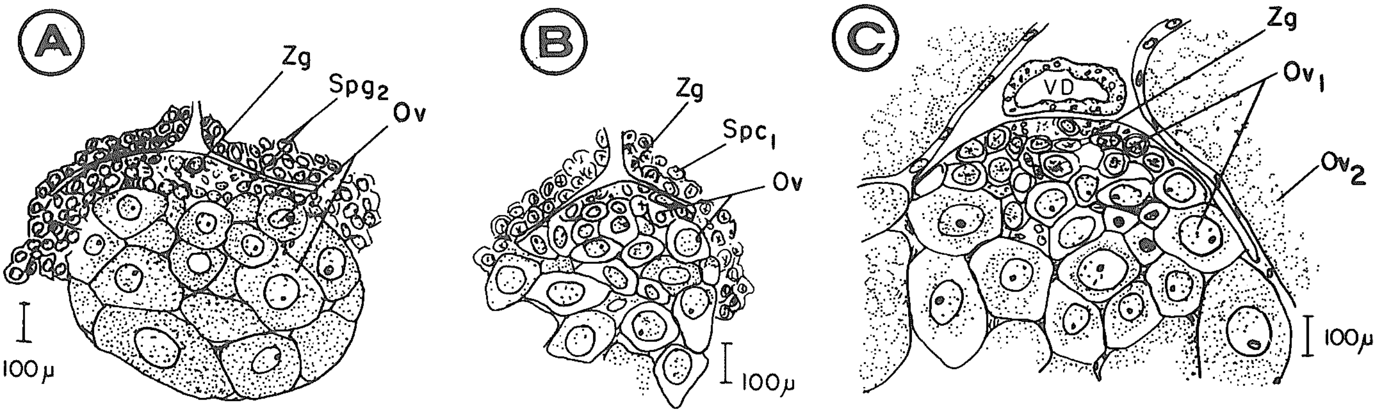

Figure 14.—A) Transverse section of the gonad of male *Pandalus borealis* in which the germinative zone functions as in the male (producing secondary spermatogonia). Spg2: secondary spermatogonia. B) Transverse section of the gonad of a male *Pandalus borealis*. The germinative zone functions as in the female (producing secondary ovogonia). Ov: ovocyte; Spc: spermatocyte; Zg: germinative zone. C) Transverse section of a female *Pandalus borealis*. Ov_1: ovocyte at the first stage of growth; Ov_2: ovocyte in vitellogenesis; VD: dorsal vessel (after Berreur-Bonnenfant and Charniaux-Cotton 1965).

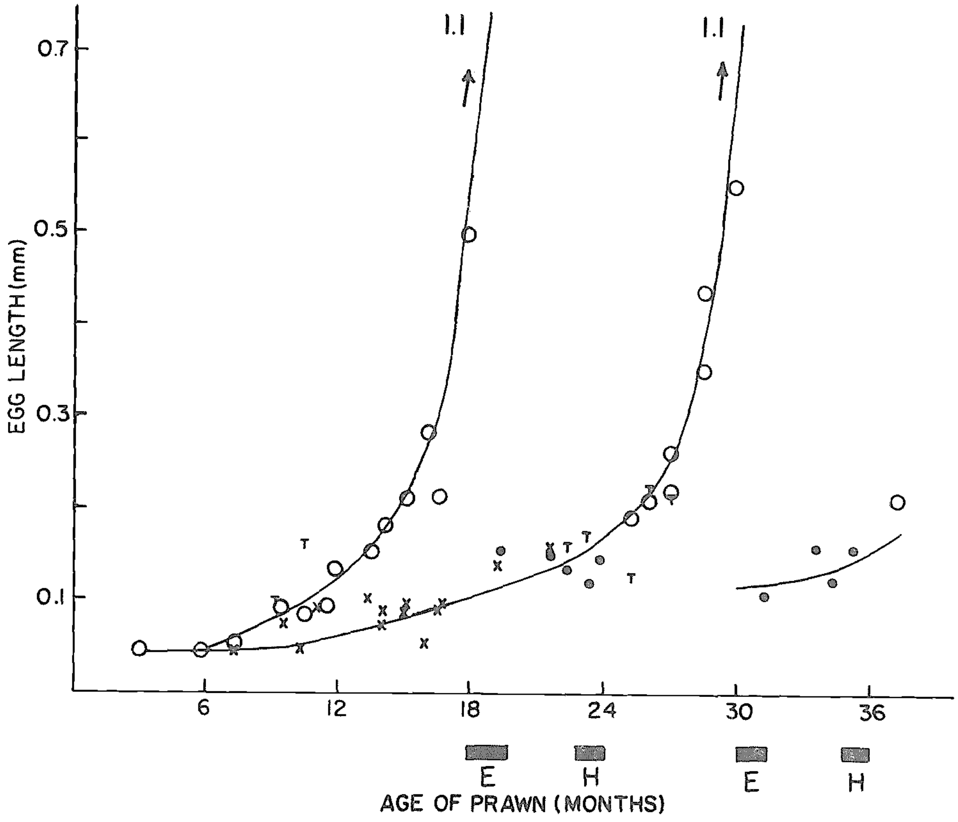

Figure 15.—Graph to show the increase in length of the oocytes (solid lines) with the age of the shrimp. The plotted lines may be continued upwards linearly, and at a size of about 1.1 mm the oocytes have developed into eggs. The symbols indicate the sex of the prawns; solid circles, female carrying eggs on the pleopods; open circles, female not carrying eggs; x, male; T, transitional; E, egg-laying; H, hatching of larvae (after Allen 1959).

Table 4.—Gradation in ovary development in four transitional stages of northern shrimp in the Gulf of Maine. Percentages in parentheses—from Haynes and Wigley (1969).

	Gradation in ovary development		
		Ova clearly visible in ovary	
Transitional stage	Ova microscopic; ovary not elongated	Ovary somewhat elongated	Ovary extending to anterior limit of cephalothorax
I			
Slight atrophy of secondary sex organs; endopodite on first pleopod not lanceolate	163 (99.4)	1 (0.6)	0 (0.0)
II			
Moderate atrophy of secondary sex organs; endopodite on first pleopod slightly lanceolate	144 (97.9)	2 (1.4)	1 (0.7)
III			
Advanced atrophy of secondary sex organs; endopodite on first pleopod nearly lanceolate	30 (39.4)	6 (8.0)	40 (52.6)
IV			
Complete or nearly complete atrophy of secondary sex organs; endopodite on first pleopod lanceolate	8 (10.0)	4 (5.0)	68 (85.0)

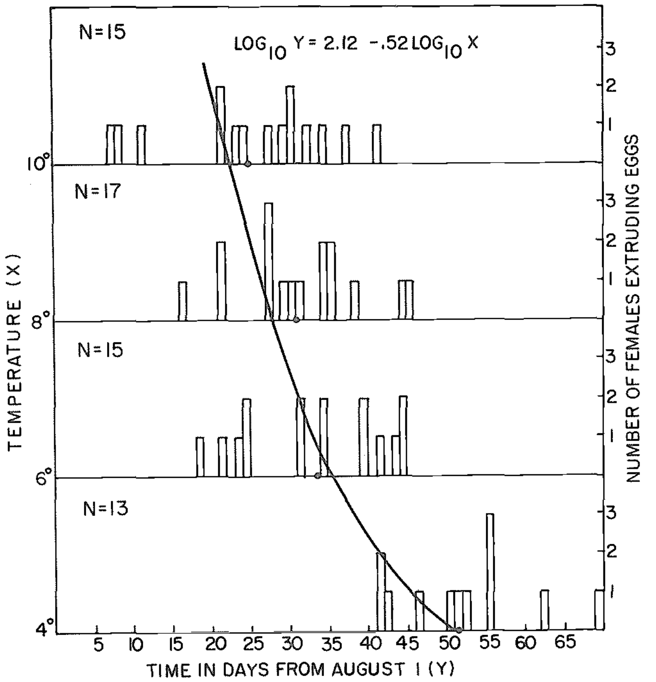

Figure 16.—Times of egg extrusion in three groups of females held at four different temperatures. All three groups were identical at the start of the experiment with respect to the developmental state of the ovaries. Vertical bars indicate the number of shrimp which extruded their eggs on any particular day. Curved line is the regression for the observed duration of ovogenesis on temperature (from Stickney and Perkins 1980).

Haynes and Wigley 1969; Horsted and Smidt 1956; Ito 1976; Rasmussen 1953; Stickney and Walton[3]). Fecundity generally increases with body size and varies depending on the age of the egg mass. Stickney and Walton (footnote 3) used a straight line relationship to relate the size of the females and the number of eggs carried (Fig. 17). This method was used for reasons of simplicity and was justified by the fact that only a portion of the whole distribution was under study and even in a curvilinear relationship this portion of the curve would be nearly straight. Further, calculated points using the straight line equation were within the error of estimate of the curvilinear equation where such comparisons were made. Rasmussen (1953), Allen (1959), Haynes and Wigley (1969), and Apollonio and Dunton (1969) (see Figs. 18, 19) found the relationship to be curvilinear. More recently, Skuladottir et al. (1978) tested the relationship between size of females and number of eggs and found that linear regressions gave the best fit to the data in all but one sample. A power curve, $y = aX^b$ also fit well and was fitted to their data as they suspected a nonlinear relationship due to scarcity of data points in the smaller length groups. Egg numbers vary with geographical area and range from 600 to 4,900 depending on the size of the female; average-sized females from most areas carry about 2,000 eggs.

Elliot (1970) found a significant decline in the number of eggs Stage I to those of Stage IV and attributed the loss to cannabalism by neighboring shrimp and to eggs being knocked off during

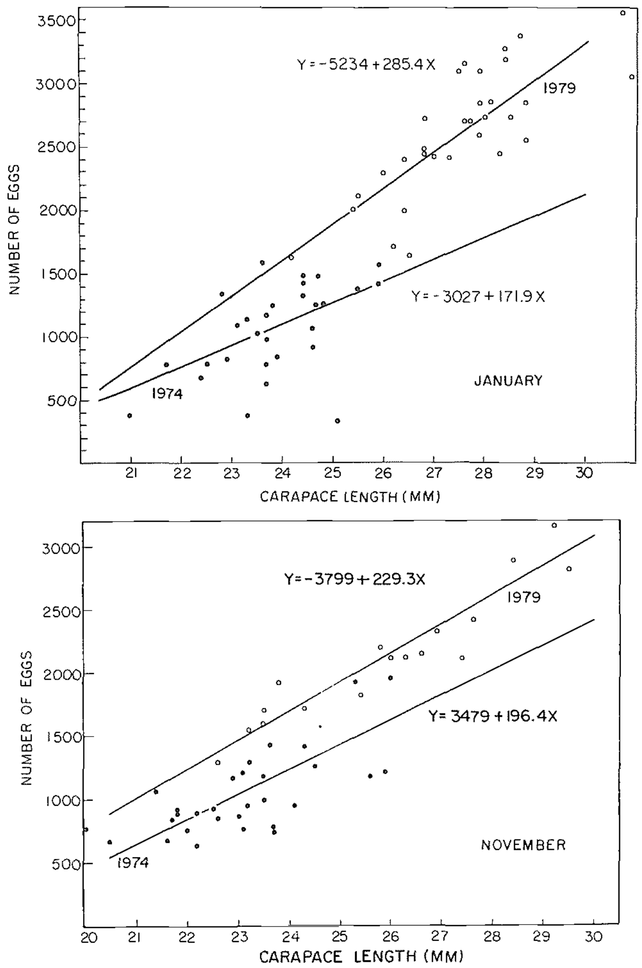

Figure 17.—Numbers of eggs carried by female *Pandalus borealis* compared for the years 1974 and 1979. The samples were collected in November of the same years. The regressions of egg number on carapace length are illustrated. Solid circles = 1974; open circles = 1979. (After Stickney and Walton footnote 3.)

scavenging activity by the parent. Skuladottir et al. (1978) noted that between September and March there was a 30-54% egg loss from females in Icelandic waters. In addition, nonviable eggs have been reported (see section 3.35).

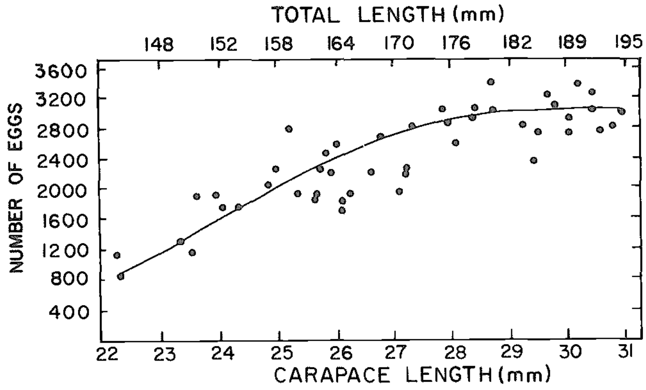

Figure 18.—Relation between the number of eggs per clutch and the size of *Pandalus borealis* from the Gulf of Maine (after Haynes and Wigley 1969).

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[3] Stickney, A. P., and C. J. Walton. Changes in fecundity of northern shrimp, *Pandalus borealis*, in the Gulf of Maine, 1964-1982. Manuscr. in prep. Department of Marine Resources, West Boothbay Harbor, ME 04575.

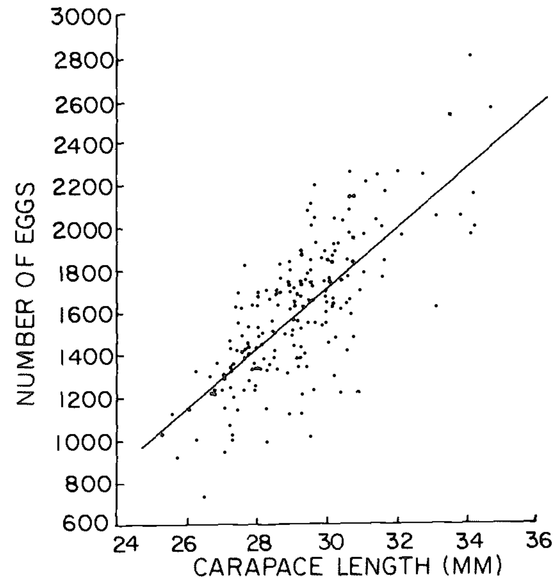

Figure 19.—Fecundity/length data for 202 shrimp collected in eight different locations in the Gulf of Maine in August and September 1968 with statistically significant least squares linear regression model $Y = -2{,}633.9 + 145.1X$ where X equals lateral carapace length (Apollonio et al. 1984).

3.2 Preadult phases

3.21 Embryonic phase

Embryonic development of *P. borealis* takes place within the egg. Haynes and Wigley (1969) classified the eggs and the water depth at which the females were taken (Table 5). The development rate may be monitored by measuring the area of the embryonic eye (Bohle 1976; Perkins 1972; and Stickney[4]) and is shown in Figure 20. At hatching the larvae are usually fully developed stage I zoeae. The developmental rate of the embryos is directly related to water temperature and increases as temperature increases (Fig. 21).

Table 5.—Mean and range of water depths at which ovigerous *Pandalus borealis* were collected in the Gulf of Maine, classified by the developmental stage of their eggs (from Haynes and Wigley 1969).

	Water depth (m)	
Egg stage	Mean	Range
a - nonsegmented blastoderm	185	113-274
b - segmented blastoderm	165	77-329
c - eyes pigmented; abdomen poorly developed	141	58-272
d - abdomen well developed; little if any yolk present	88	9-179

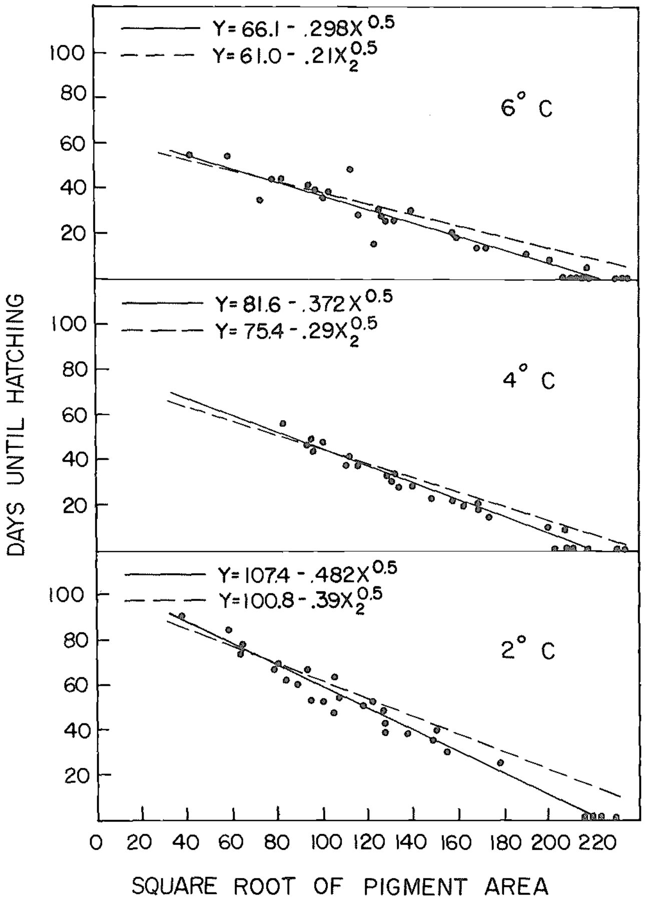

Figure 20.—Relation between the eye pigment size in eggs of *Pandalus borealis* and the length of time remaining until first hatching: regressions at three temperatures of time in days on the square root of pigment area in micrometers. Solid lines indicate the simple regressions. Dashed lines are calculated from multiple regressions which include a factor for time spent under laboratory conditions. To obtain the lines shown, this factor was given a value of zero to represent the expected relationship in the natural environment (from Stickney and Perkins 1978).

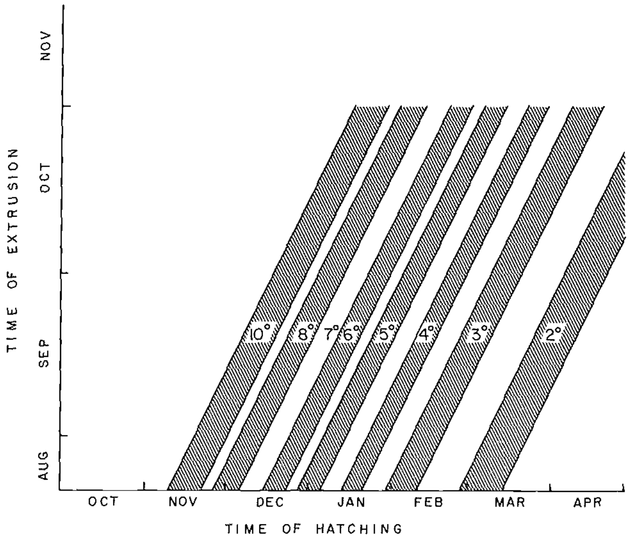

Figure 21.—The calculated hatching periods for eggs of *Pandalus borealis* at selected incubation temperatures for various times of extrusion (Stickney and Perkins unpubl. data).

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[4] Stickney, A. P. 1982. Prediction of hatching time for eggs of northern shrimp (*Pandalus borealis*) from measurement of eye pigment spots of the embryos. Unpubl. manuscr., 13 p. Department of Marine Resources, West Boothbay Harbor, ME 04575.

3.22 Larval phases

Berkeley (1930) gave the first full description of the larvae of *P. borealis* and Haynes (1979) reared the various stages and also gave a full description. Perkins (pers. obs.) found six larval stages in the Gulf of Maine during his experimental work with larvae of *P. borealis*. Both Berkeley and Haynes noted six larval stages. Wienberg (1980, 1982b) described and illustrated 11 zoeal stages and 1 postlarva. He referred to Berkeley's original description but apparently was unaware of Haynes more recent description. Lebour (1940) divided the genus *Pandalus* into two groups; one with pereiopods rudimentary on hatching and with the distal tip of the antennal scale jointed; the other group with "functional" pereiopods on hatching and the distal tip of the antennal scale unjointed. Lebour stated that *P. borealis* (presumably on the basis of Berkeley's description) was intermediate between the two groups as the species had rudimentary pereiopods on hatching but not a segmented antennal scale. Haynes, in his description of the various stages, clearly shows (his figure 1C, page 158) a jointed antennal scale in stage I larvae.

Perkins (pers. obs.) reared many larvae from female *P. borealis* from the Gulf of Maine and could not discern the segments on the antennal scale on fresh or preserved larvae but examination of larval exuvia showed the segments clearly. This character would therefore place *P. borealis* in Lebour's group one in the genus. *Pandalus borealis* has six larval stages with stage VI defined as a megalopa. The following larval description is summarized from Berkeley (1930) who described the larvae from the plankton (see Fig. 22).

Stage	*Description*
I	Eyes sessile, pereiopods undeveloped
II	Eyes stalked, basal part of antenna I segmented, pereiopods developed
III	Rostrum with teeth, uropods free, telson with one pair of lateral spines
IV	Outer flagellum of the first antenna segmented, pleopods with two segments, first pleopod undeveloped with one branch
V	Chelae on pereiopod I, plumose setae on the pleopods, inner flagellum of the first antenna segmented
VI	Appendices internae on the pleopods, ventral teeth on the rostrum
P	Postlarvae

Several aspects of the biology of larval and juvenile *P. borealis* have been studied by Stickney and Perkins (unpubl. data) and are summarized below.

Molting frequency and development of larval and juvenile shrimp

Stickney and Perkins (1977) found that larvae reared in beakers exhibited different developmental patterns than those reared in compartmented trays. They concluded that normal sequential development of the larvae terminates at the seventh stage, or after six molts, when the juvenile condition (metamorphosis) is reached. Haynes (1979) confirmed this observation. Of the larvae reared in mass culture by Stickney and Perkins, apparently no individual reached the juvenile condition until it had molted at least seven times while 78% (73 out of 94) of the viable animals reared in compartmented trays became juveniles after six molts. Figure 23 illustrates the difference in time and number of molts required by the larvae to reach the juvenile condition under the different culture methods at each temperature. The duration of intermolt periods for animals in either culture condition, within the same temperature were essentially the same but increased significantly with increasing temperature. Progressive intermolt periods at the same temperature increased significantly with the increased age of the animals.

Individuals were considered to have reached the juvenile condition when the exopods of the pereiopods were lost and natatory locomotion was primarily achieved by the pleopods. Loss of the exopods and start of pleopodal locomotion were invariably simultaneous in animals assumed to have undergone normal development.

Only those animals which reached the juvenile condition after six molts or at the seventh stage were considered as having undergone normal development, and their molting frequencies for the first nine molts at each temperature are given in Table 6. It is interesting to note the significant increase of the last larval intermolt period, between stages six and seven, at all temperatures. The total number of days required for those individuals which reached juvenile condition at the seventh stage are plotted against their individual rearing temperatures in Figure 24.

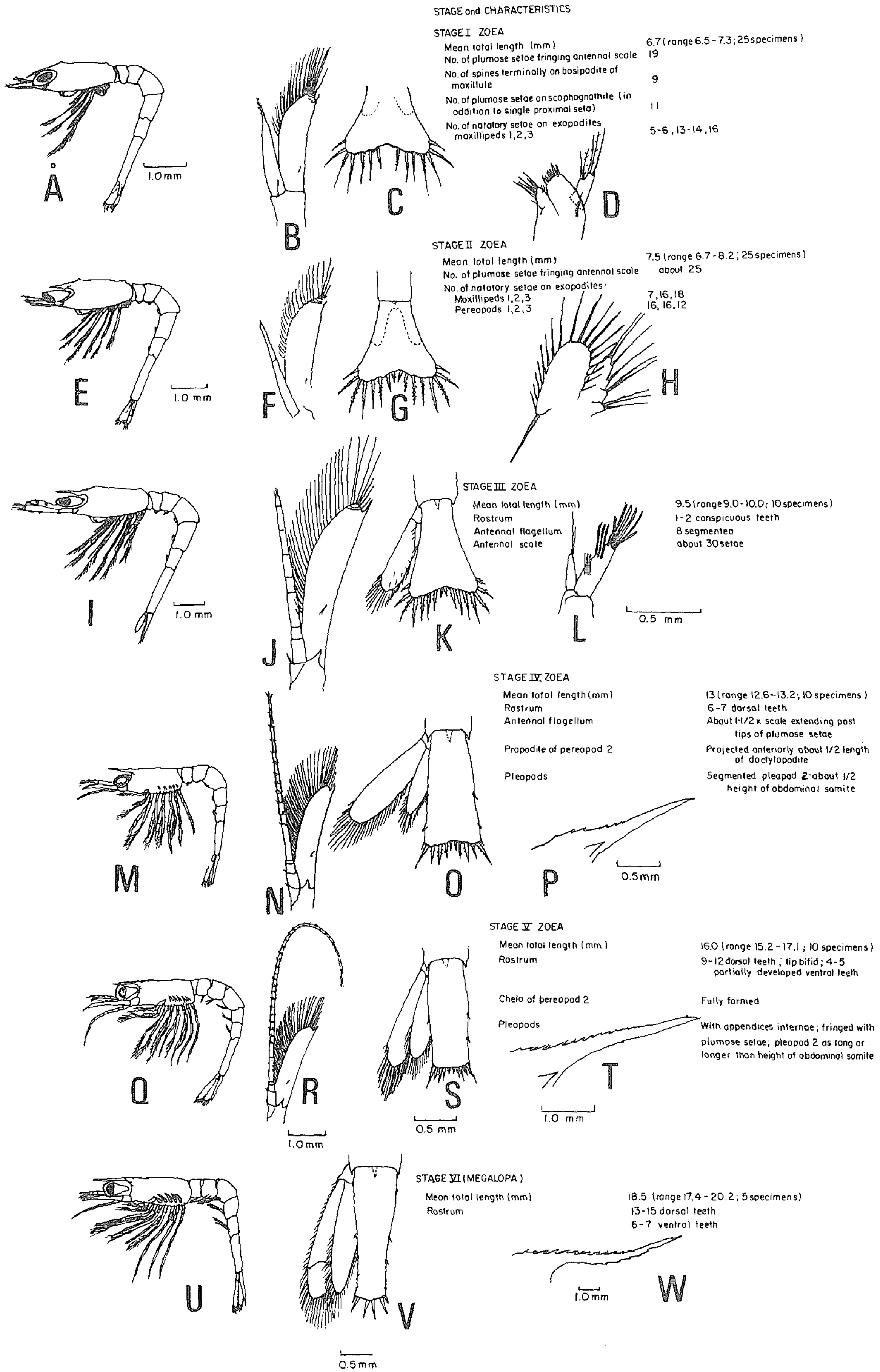
A total of 24 juvenile shrimp, 7 mo in age, were set up, six animals per temperature, at 4° (4.0°-4.5°), 6° (6.1°-6.6°), 8° (7.9°-8.5°), and 10° (10.0°-10.3°) C. The juveniles were placed in individual cubicles, water was constantly circulated through each cubicle, and food was given periodically in measured amounts. Water temperature had a significant effect on molting frequencies over the total range of the experimental temperatures; molting frequency generally increased as temperature increased. However, within each temperature regime there was considerable variation in molting frequency among the individuals. These differences were mainly attributable to the size of the individual animals: the larger the juvenile, the greater its intermolt periods at a given temperature. Average intermolt periods for juvenile shrimp whose carapace lengths ranged from 6 to 9 mm the first year and from 9 to 12 mm the second year, at 4°, 6°, 8°, and 10°C were, in days, 39, 33, 28, and 24, respectively, for the first year, and 48, 43, 38, and 34 the second year.

Growth

Stickney and Perkins (1977) held individual larvae and juveniles in compartmented trays to compile data on growth of larval and early juvenile shrimp. Each time an animal molted, the exuvia, if attainable, was removed and measured with an ocular micrometer. Carapace length was measured along the dorsal midline, from the posterior edge of the eye socket to the posterior edge of the carapace. Only data from those individuals which underwent normal development were used.

No significant difference ($P > 0.05$) in carapace length, at the same stage, was evident from the effect of the different rearing temperatures. As no significant differences were found, measurements of carapace length were combined from animals at all temperatures, at each stage, and are presented in Table 7. A rather drastic reduction in the relative increase in carapace length occurs when the juvenile condition is reached. This reduction probably reflects a change in body shape as metamorphosis is reached, rather than being an artifact of laboratory culture. Haynes (1979) found the same type of reduction in late larvae and early juveniles reared in situ.

As molting frequency increased with higher temperature, growth with time also increased with temperature. The relation-



STAGE and CHARACTERISTICS

STAGE I ZOEA

Mean total length (mm)	6.7 (range 6.5 - 7.3; 25 specimens)
No. of plumose setae fringing antennal scale	19
No. of spines terminally on basipodite of maxillule	9
No. of plumose setae on scaphognathite (in addition to single proximal seta)	11
No. of natatory setae on exopodites maxillipeds 1,2,3	5-6, 13-14, 16

STAGE II ZOEA

Mean total length (mm)	7.5 (range 6.7 - 8.2; 25 specimens)
No. of plumose setae fringing antennal scale	about 25
No. of natatory setae on exopodites:	
Maxillipeds 1,2,3	7, 16, 18
Pereopods 1,2,3	16, 16, 12

STAGE III ZOEA

Mean total length (mm)	9.5 (range 9.0 - 10.0; 10 specimens)
Rostrum	1-2 conspicuous teeth
Antennal flagellum	8 segmented
Antennal scale	about 30 setae

STAGE IV ZOEA

Mean total length (mm)	13 (range 12.6-13.2; 10 specimens)
Rostrum	6-7 dorsal teeth
Antennal flagellum	About 1-1/2 x scale extending past tips of plumose setae
Propodite of pereopod 2	Projected anteriorly about 1/2 length of dactylopodite
Pleopods	Segmented pleopod 2-about 1/2 height of abdominal somite

STAGE V ZOEA

Mean total length (mm)	16.0 (range 15.2 - 17.1; 10 specimens)
Rostrum	9-12 dorsal teeth; tip bifid; 4-5 partially developed ventral teeth
Chela of pereopod 2	Fully formed
Pleopods	With appendices internae; fringed with plumose setae; pleopod 2 as long or longer than height of abdominal somite

STAGE VI (MEGALOPA)

Mean total length (mm)	18.5 (range 17.4 - 20.2; 5 specimens)
Rostrum	13-15 dorsal teeth 6-7 ventral teeth

Figure 22.—Larval development of *Pandalus borealis* (after Berkeley 1930; Haynes 1979).

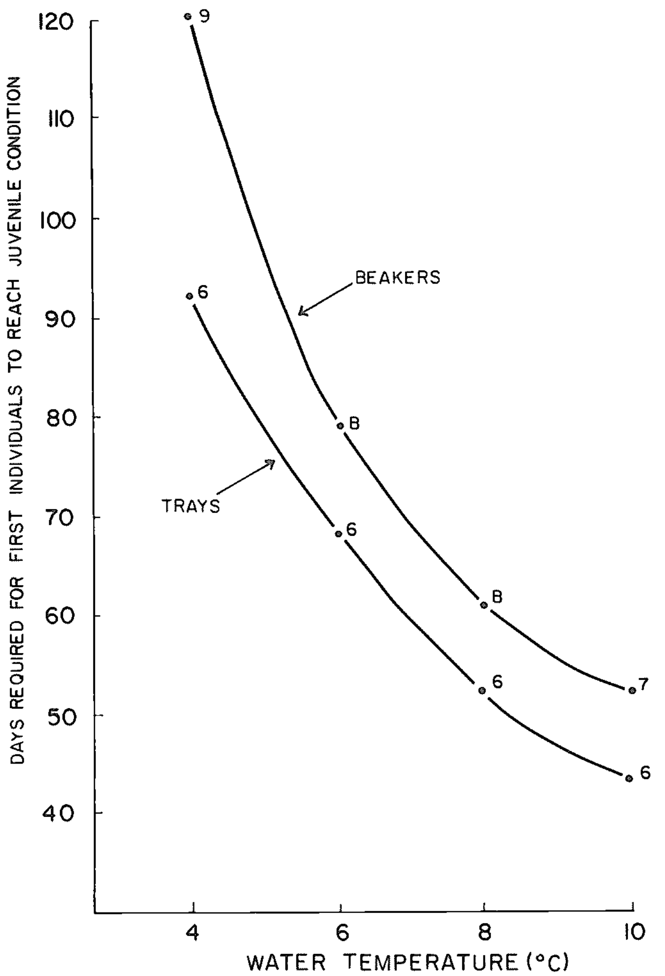


Figure 23.—The number of days required for larvae of *Pandalus borealis* to reach metamorphosis under two cultural conditions at four experimental temperatures. The number next to each point indicates the number of molts required to reach metamorphosis at the given condition (from Stickney and Perkins 1977).

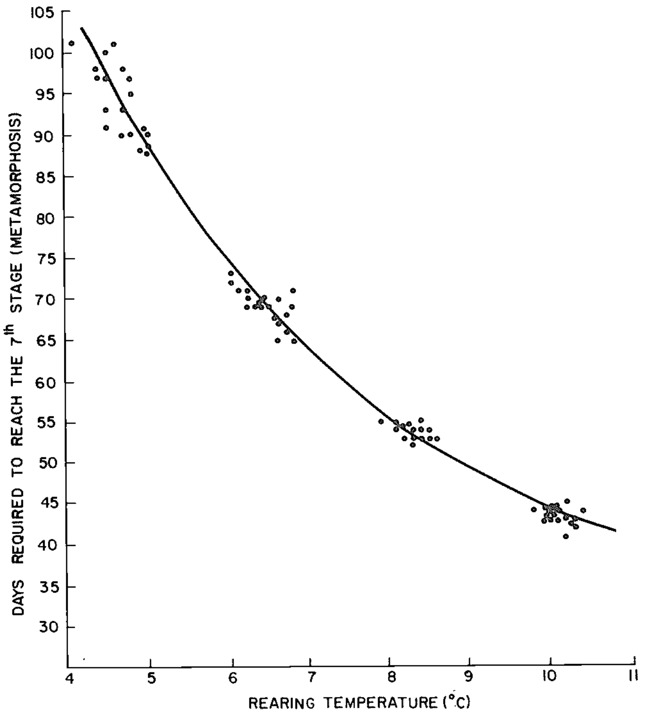


Figure 24.—The total number of days required for larvae of *Pandalus borealis* to reach metamorphosis plotted against their average individual rearing temperature (from Stickney and Perkins 1977).

ship between the rate of growth and rearing temperature is shown in Figure 25. The greatest value of these growth data is to show the differences, or lack of differences, in growth that may be attributable to water temperature. The actual size of these artificially reared animals at a fixed point in their development or in time should not necessarily be regarded as representative of values for animals in natural populations. Culture environment can have a significant effect on growth as well as development, and of the two culture methods employed, animals reared individually in

Table 6.—The time in mean number of days required by larval and early juvenile *Pandalus borealis* to reach successive stages at four experimental temperatures.

Temperature (°C) range	Stage								
	2	3	4	5	6	7	8	9	10
"4°"									
(4.1-5.0)	11.6	12.0	13.7	14.9	16.7	25.0	24.2	25.2	24.2
Standard deviation	1.38	0.78	0.93	0.74	0.87	1.73	1.57	1.67	0.50
Accumulative days		23.6	37.3	52.2	68.9	93.9	118.1	143.3	167.5
Standard deviation		1.80	2.56	2.76	3.32	4.58	5.46	4.45	4.11
"6°"									
(6.0-6.8)	8.6	9.2	10.2	10.8	12.7	17.5	17.6	18.0	17.5
Standard deviation	0.68	0.63	0.63	0.63	0.73	0.61	1.01	1.93	1.05
Accumulative days		17.8	28.0	38.8	51.5	69.0	86.6	104.6	122.1
Standard deviation		1.12	1.39	1.46	1.98	2.12	2.57	3.48	2.93
"8°"									
(7.9-8.6)	6.8	7.2	7.6	8.1	9.7	14.5	13.9	14.9	15.1
Standard deviation	0.40	0.54	0.51	0.36	0.48	0.63	0.96	1.12	1.10
Accumulative days		14.0	21.6	29.7	39.4	53.9	67.8	82.7	97.8
Standard deviation		0.52	0.51	0.73	0.68	0.86	1.45	1.77	1.67
"10°"									
(9.8-10.4)	5.4	5.6	6.0	6.7	8.0	11.5	11.5	12.7	12.7
Standard deviation	0.61	0.50	0.52	0.67	0.62	0.61	0.82	1.16	0.82
Accumulative days		11.0	17.0	23.7	31.7	43.2	54.7	67.4	80.1
Standard deviation		0.52	0.81	0.79	0.96	0.95	1.18	1.92	2.05

Table 7.—The average carapace length measurements, by stage, of larval and juvenile *Pandalus borealis* reared under laboratory conditions (Stickney and Perkins 1977).

Stage	Number of measurements	Mean carapace length (mm)	SD	Percentage increase in carapace length by stage
1	40	1.42	0.099	
2	20	1.61	.079	13.3
3	39	2.04	.108	26.7
4	76	2.40	.144	17.8
5	71	2.86	.179	19.2
6	73	3.15	.160	10.1
7	72	3.22	.186	2.2
8	61	3.40	.192	5.6
9	44	3.61	.205	6.2
10	34	3.82	.216	5.8
11	33	3.99	.252	4.5
12	27	4.23	.300	6.0
13	24	4.45	.338	5.2
14	16	4.70	.297	5.6

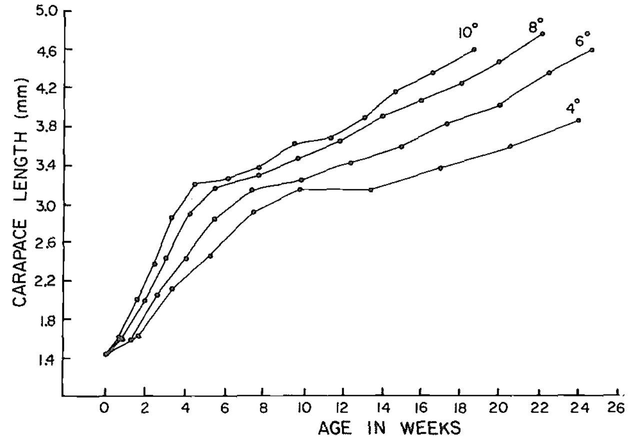


Figure 25.—Growth rates of larvae and early juveniles of *Pandalus borealis* at four experimental temperatures. Each point indicates a molt of stage (from Stickney and Perkins 1977).

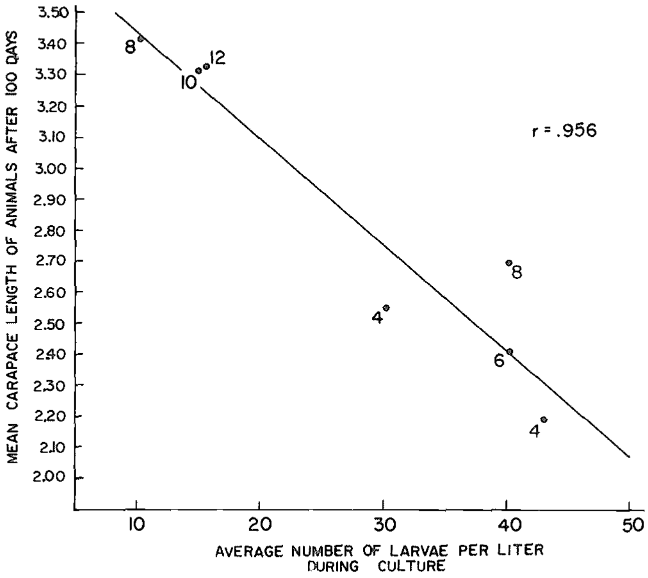


Figure 26.—Mean carapace length obtained after 100 d by the various groups of experimental animals plotted against the average number of larvae per liter in the culture media for that period. Culture temperature for each value is indicated next to the points on the graph (from Stickney and Perkins 1975).

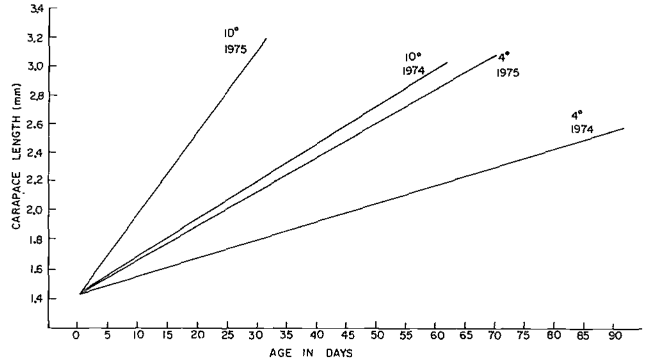


Figure 27.—The trends of growth of larvae of *Pandalus borealis* reared under different cultural conditions at two temperatures. Lines labeled 1974 indicate beaker culture; lines labeled 1975 indicate culture in compartmented trays (from Stickney and Perkins 1977).

compartmented trays grew better than those reared in mass culture in beakers where the density of larvae also had a direct effect on the growth of the individuals (Fig. 26). The difference in trends of growth for larvae reared under both conditions, at two temperatures is shown in Figure 27.

The 24 juvenile shrimp previously mentioned under the section on molting and development were used to measure the effects that the amount and rate of food consumption had on the growth of juvenile shrimp held at experimental temperatures of 4°, 6°, 8°, and 10°C. Six juveniles were held at each temperature; three animals at each temperature were periodically fed pieces of mussel gonad, the other three whole mysids. Although no significant differences in food intake or growth could be found for animals within the same temperature, feeding rate and growth were both more rapid as temperature increased. This increased rate of feeding and growth with temperature does not imply that the warmer temperatures were necessarily more beneficial to the juveniles held at those temperatures. The total amount of food eaten by the juveniles over the first six molting periods was approximately the same regardless of temperature, and no significant differences could be found in the total growth of the animals after six molts within or between temperatures. As mentioned previously, growth rate was greater as temperature increased, and conversely intermolt periods become greater as temperature decreases. Juveniles at 4°C averaged 260 d to complete six molts; those at 10°C averaged 148 d. The rate of food consumption per day was therefore much higher (3.00 mg/d) at 10° than at 4° (1.7 mg/d). When the mean increase in carapace length for the six molts for all animals at each temperature was divided by the daily rate of food intake the effect of temperature becomes apparent and is shown in Figure 28. The figure illustrates the increase in growth by rate of food consumption at the four experimental temperatures (both food types combined). It is evident, therefore, that at least within these thermal limits, the juvenile shrimp were expending progressively more energy for metabolic processes as temperature increased and that that expenditure could have an important effect on their growth if food were not ingested in proportionately greater quantities at the warmer temperatures.

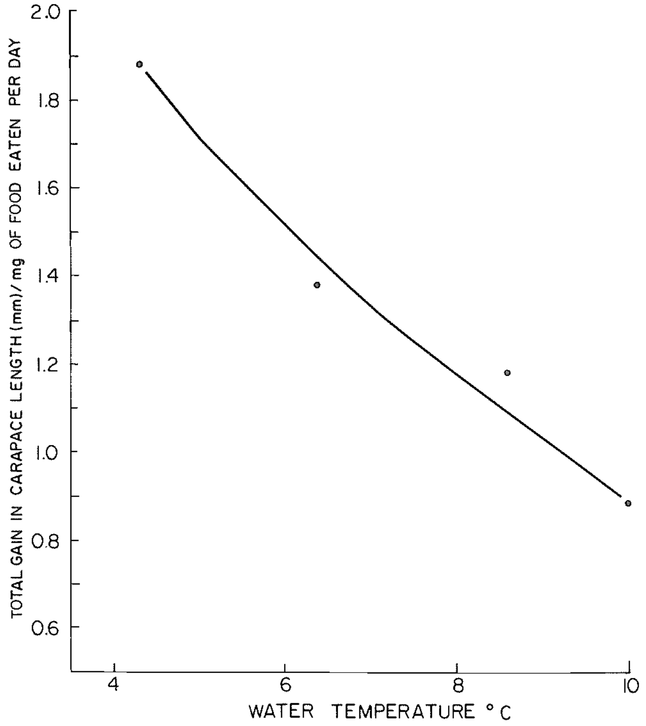


Figure 28.—The relative increase in carapace length by amount of food eaten, after six molts, for juveniles of *Pandalus borealis* at four experimental temperatures (from Stickney and Perkins 1977).

Survival and development of larvae on natural plankton

Although shrimp larvae survive and grow reasonably well when provided rather dense populations of artificially cultured organisms, it is upon much sparser populations of mixed species that they must feed and survive in nature. For a limited time during the months of March and April, Stickney and Perkins (1977) monitored daily plankton in the Boothbay Harbor seawater to determine its density and taxonomic make-up. The resulting plankton was fed to newly hatched shrimp larvae in natural and in artificially augmented densities, to see whether typical surface water plankton of the season could provide an adequate diet.

Replicate cultures of 14 first stage larvae in 2.5 L glass containers were fed every day to maintain the following food densities: no food; unconcentrated natural harbor plankton; 2 times harbor plankton density; and 4 times harbor plankton density. Replicate, fed controls contained densities of approximately 1,000 *Artemia* nauplii per liter. The cultures were maintained at 4°C, approximately equivalent to the seasonal natural water temperature. Concentrations of natural plankton were made by straining known volumes of raw harbor water through a fine mesh (50 μm opening) screen and washing the accumulated plankton into appropriate volumes of filtered seawater.

Only the larvae fed *Artemia* survived and developed. Most of them reached the second stage and at the end of a month 62% of them were alive and vigorous. All others had died after this period, although even in the unfed controls there was one survivor (in very poor condition) after 28 d. The survival curves for the various cultures appeared to fall into three categories. The unfed controls died off at the fastest rate. The group fed natural plankton in natural density died off at the next fastest rate, but, surprisingly, the group fed *Artemia* died off at very nearly the same rate at first, although after this initial period of mortality very few additional ones died. Those fed 2 and 4 times the natural plankton density survived best at first, but died off precipitously at 20 d.

From 25 March to 10 April, the natural plankton density of organisms between 50 and 500 μm did not exceed 1,000/L and only once exceeded 500/L. It was not until 15 April that natural "food" concentrations remained consistently higher than 1,000/L: not until 2 wk after the larvae had hatched. It has been shown that starved larvae reached a "point of no return" after which, even though still living and eventually provided with adequate food, they will not survive. It is likely that this situation occurred here—that even 4 times the natural plankton was not adequate during the first few days of larval life. During the first week, for instance, the natural "food" density was generally < 100 organisms/L. Concentrations of 1,000/L of some food organisms are adequate to sustain larval growth, e.g., *Artemia*. But these are relatively large organisms. A concentration of 1,000/L ensures the probability of a certain number of individual food items being captured by the shrimp larvae; it does not ensure the adequacy of these as food. To provide the quantity of nutrition necessary much higher concentrations of food organisms smaller than *Artemia* would seem to be required.

It is the interaction between the probability of catching the food organisms and their value as food that probably accounts for some of the anomalies in the survival curves in Figure 29. The larvae fed *Artemia* died almost as frequently as the most poorly fed larvae during the first 18 d; thereafter the survivors continued to survive while the survivors in all other cultures continued to die

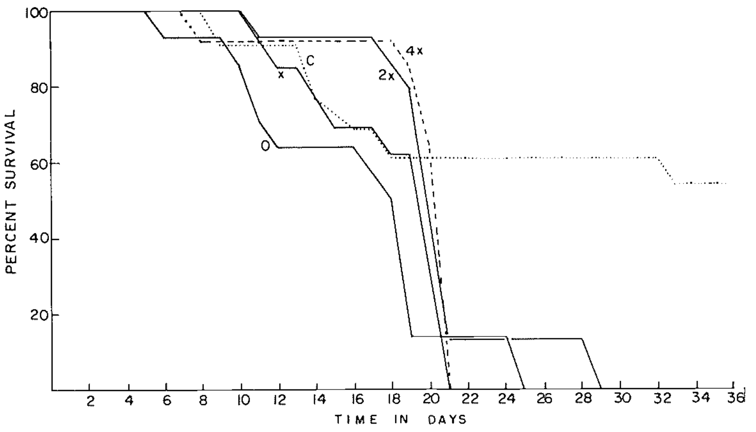


Figure 29.—Survival curves for newly hatched larvae of *Pandalus borealis* supplied with three different concentrations of natural plankton as food. O: unfed control; C: control fed *Artemia* nauplii; X: fed natural plankton at normal seasonal density; 2X: fed natural plankton at twice normal density; 4X: fed natural plankton at four times normal density (from Stickney and Perkins 1977).

off. From this Stickney and Perkins (1977) inferred that the 2 and 4 times natural plankton concentrations are sufficient to ensure a fairly high probability of capture, but most of them, once caught, are nutritionally inadequate. In the *Artemia*-fed cultures, the probability of catching food was not high enough to ensure that every individual larva obtained a meal before it reached the point of no return. The unsuccessful larvae died. Those successful individuals obtained enough nourishment from the first few *Artemia* nauplii they caught to sustain them for the waiting periods between catches.

Stickney and Perkins (1977) calculated survival rates from plankton tows taken throughout the larval period in the coastal waters of Maine during several years. The trends of survival in nature closely parallelled the trend of unfed laboratory cultures of larvae (Fig. 30).

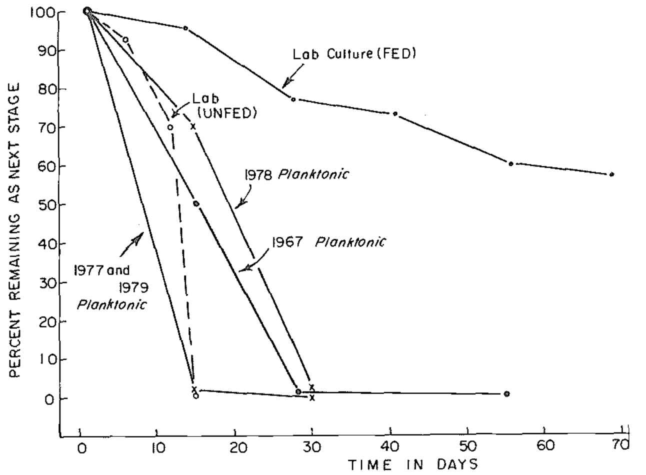


Figure 30.—Comparisons of survival trends between fed and unfed laboratory cultures of larval *Pandalus borealis* and survival of naturally occurring larvae observed from sequential plankton tows during several years.

Survival

Stickney and Perkins (1977) conducted studies to determine the trends of larval and early juvenile survival using several culture techniques. Newly hatched shrimp were cultured in 3 L beakers of filtered seawater throughout most or all of their larval period and were then placed in compartmented trays during experiments conducted in 1974. During 1975 the newly hatched larvae were cultured throughout all their larval and early juvenile periods in compartmented trays. Starting densities of larvae in the beakers during 1974 ranged from 30 to 70 individuals/L. Animals reared in trays were each confined in separate compartments containing 100 ml of filtered seawater. All seawater used in these experiments was changed every other day. Coarse air bubbles were constantly administered to the cultures in beakers to insure mixing of the larvae and food. Newly hatched brine shrimp (*Artemia*) nauplii were provided as food in densities of approximately 1,000/L and were replenished every other day. The animals were cultured at 4°, 6°, 8°, and 10°C during both years. A few additional larvae were cultured at 12° and 15°C during 1974.

The trends of survival at the various temperatures and by culture method are given in Figure 31. The rate of survival for those larvae reared in beakers at 12° was essentially the same as was that for larvae held at 10°; larvae cultured at 15° were all dead after 43 d.

Mortality was generally more rapid during the first few weeks at the higher temperatures; it was also greater and earlier at the same temperature in animals reared in compartmented trays. The chi-square value derived from the number of survivors after 100 d among all the experimental temperatures, for both years, was significant ($P < 0.05$). When the effect of survival at 4°C was removed from the calculations, however, the resulting chi-square value was not significant. The chi-square value for survival in 1975 after 160 d among all temperatures was not significant. Weinberg (1982a) found similar survival rates at temperatures between 3° and 9°C (Fig. 32).

The early survival rates at three temperatures for fed and unfed larvae are given in Figure 33. These larvae were kept in compartmented trays: one larva per compartment of 100 ml filtered seawater. As noted previously, mortality was greater in the early larval period as temperature increased, and regardless of whether or not the animals had food available, mortality rate was similar during this early period. Stickney and Perkins (1977) concluded that this similarity in mortality rate was due to the lack of feeding, or the lack of sufficient feeding, by many of the larvae that had food available. That the curves of survival for animals that had food available leveled with time was an indication that the residual

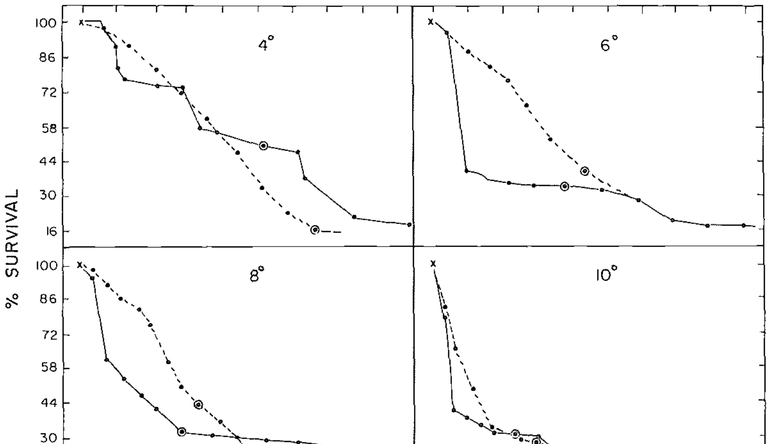


Figure 31.—The trends of survival for larval and early juvenile *Pandalus borealis* at four experimental temperatures. Dashed lines indicate trends of survival for animals reared in beakers (1974); solid lines are for animals reared in compartmental trays (1975). The circled points indicate the points at which metamorphosis was reached (from Stickney and Perkins 1977).

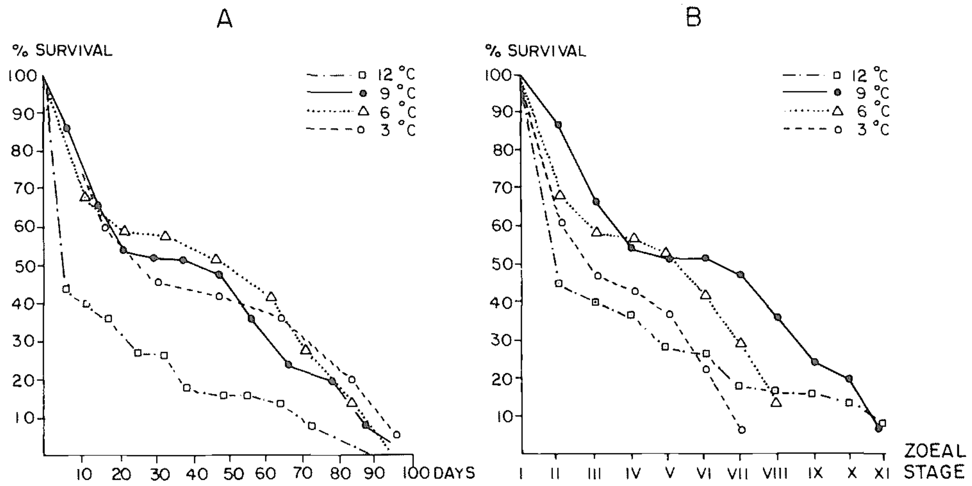


Figure 32.—A) Survival according to age (in days after hatching) of laboratory reared *Pandalus borealis* larvae at different temperatures; and B) survival according to zoeal stage of laboratory reared *Pandalus borealis* larvae at different temperatures (from Weinberg 1982a).

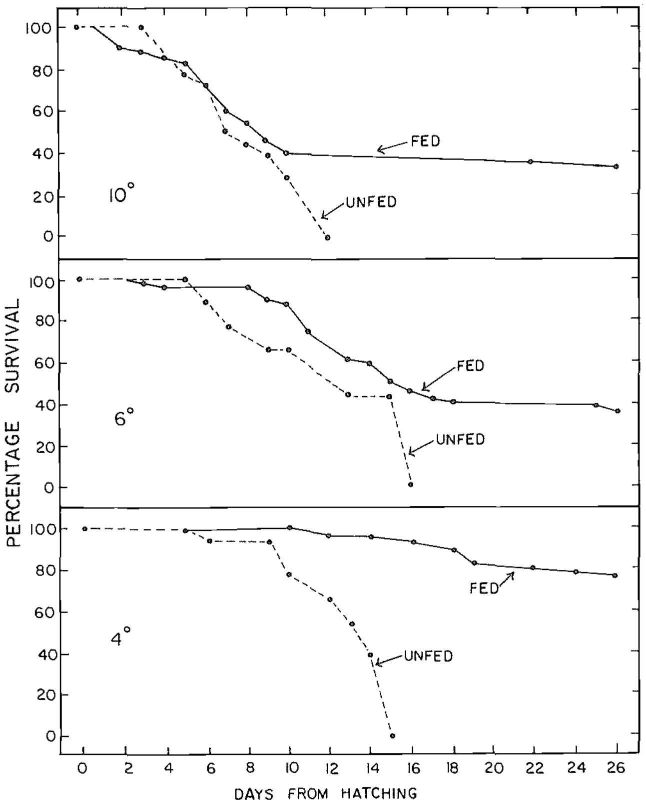


Figure 33.—Survival trends during the early larval period of fed and unfed larvae of *Pandalus borealis* at three experimental temperatures (from Stickney and Perkins 1977).

animals had initially obtained sufficient food. The lack of drastic early mortality at 4°C among the larvae that had food available was probably due to the decreased metabolic requirements of the animals at that temperature, i.e., the need for immediate ingestion or the amount of ingestion of food was not as critical at the reduced temperature. In Figure 31 it can be noted that the general trend of early mortality was greater in those animals cultured in compartmented trays. It was concluded the larvae cultured in beakers had a greater chance of coming in contact with food as the water was kept in motion in the beakers from the air bubbles, this insuring mixing of the *Artemia* nauplii and the larval shrimp. In the compartments, where there was little or no water movement, the larvae had to seek their food and probably were not as successful at it as were those in the beakers.

The ability and inclination of a larva to feed shortly after hatching, and to continue feeding, are of course of primary importance if the larva is to survive at all. During 1976 and early 1977 preliminary experiments were conducted by Stickney and Perkins (1977) to determine the amount and rate of food intake needed by larval shrimp to survive and the critical duration after hatching in which a larva must obtain food before the "point of no return" or consequental death is reached. The experiments to determine feeding rates were conducted using compartmented trays with 100 ml of filtered seawater with *Artemia* nauplii in manually counted concentrations (10-200/L) added to each compartment. One larva was put into each compartment and remaining food was counted periodically to determine feeding rates. The experiments conducted to determine the length of time larvae can go without feeding after they hatch, provided they eventually obtain food and survive, were done in the same manner except that food was withheld from the larvae for various periods (2-48 h) after they had hatched. At temperatures of 4° to 5°C preliminary results indicate a larva must ingest at least some food within 30 h after hatching or death is insured even though food is obtained thereafter. Within this same temperature range, larvae must obtain food in the amount and quality of 4 *Artemia* nauplii/d in order to survive for even a few weeks and larvae need approximately 10 *Artemia* nauplii/d to maintain life through the first few molts. These requirements increase as the animal grows and as temperature increases. The act of molting is, in itself, a time of considerable stress. The feeding rate of larval shrimp decreases shortly before a molt, then picks up again after completion of the molt. A molt must be preceded by sufficient nutritional intake not only to carry the animal through the molt but also to insure enough energy reserve to enable the early resumption of postmolt feeding. Many newly hatched larvae will eventually molt once even after complete starvation, the result is, of course, death. Many larvae will consume small amounts of premolt food, cease feeding, and molt but be too weakened to resume feeding and die. Other larvae will eat apparently sufficient amounts of food prior to a molt, then molt, but not resume feeding for perhaps a day, and then only in small amounts; these larvae invariably die within a few days. Obviously only those larvae which have ingested food of the necessary amount and quality can survive.

Paul et al. (1979) observed the daily consumption rates of copepods by the larvae of three crustaceans including *P. borealis* (Table 8) and Stickney and Perkins (1981) examined the intestinal tracks of larval *P. borealis* from plankton tows and listed the various food items found (Table 9). Stickney and Perkins (1979) reported VO_2 values for stage I larvae of *P. borealis* of 6.5, 9.4, and 16 μLO_2/larva per d at 2.6°, 4.0°, and 6.5°C, respectively. The values are in close agreement with the results of Paul and Nunes (1983) who later observed the oxygen consumption rates and metabolic requirements of larval *P. borealis* at various temperatures (Table 10, Fig. 34).

Wienberg (1982a) found an optimal culture temperature of 9°C with increasing growth and molting frequency as temperature increased and as temperature decreased the amount of food consumed decreased. He also noted that larvae held in constant darkness had the same mortality and growth rates as those held in a 12-h light-dark rhythm. Wienberg found that salinities from 31 to $32^{0}/_{00}$ were optimal for the larvae and that growth and feeding rate declined at salinities below $28^{0}/_{00}$.

Table 8.—The average daily consumption of copepods by stage-one zoeae of king crab, snow crab, and pink shrimp (from Paul et al. 1979).

	Prey concentration per liter			
	20	40	80	160
King crab				
Mean	0.8	1.3	2.6	7.6
SD	0.9	0.8	1.8	2.8
SE	0.2	0.3	0.5	0.9
Range	0.0-2.0	0.0-2.3	1.0-7.0	3.0-12.0
Snow crab				
Mean	0.5	1.3	2.2	4.8
SD	0.3	0.6	1.1	1.8
SE	0.1	0.2	0.4	0.6
Range	0.0-1.0	0.4-2.0	1.0-4.0	2.0-7.0
Pink shrimp				
Mean	0.7	1.5	2.3	5.3
SD	0.4	0.7	1.2	2.1
SE	0.2	0.2	0.4	0.7
Range	0.2-1.0	0.6-2.8	1.0-4.0	2.4-9.6

Table 9.—Stomach contents of larval shrimp, 1979. The number of individuals and the percent ( ) of sample in which the listed food categories were found. First and second stages are combined. After Stickney and Perkins (1981).

Date	2-28-79	3-13-79	3-21-79	3-28-79	Total
Number examined	30 (100%)	40 (100%)	40 (100%)	16 (100%)	126 (100%)
Food category:					
Diatoms, all kinds	15 (50)	21 (53)	11 (28)	12 (75)	59 (47)
Coscinodiscus	6 (20)	4 (10)	1 (3)	4 (25)	15 (12)
Crustacea	4 (13)	0 (0)	3 (8)	2 (13)	9 (7)
Polychaetes	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Other invertebrates	2 (7)	0 (0)	3 (8)	1 (6)	6 (5)
Any food, identifiable or not	29 (97%)	37 (93%)	33 (83%)	15 (94%)	114 (90%)

Table 10.—Oxygen consumption of stage-one zoeae of *Pandalus borealis* (from Paul and Nunes 1983).

Temperature (°C)	Oxygen consumption		Mean dry wt. zoeae (mg)
	μLO_2/mg per h	$\mu LO_2 \cdot 0.17$ mg/ind. per h	
1.5			
Mean	1.54	0.26	0.17
SD	0.74	0.12	0.01
Range	1.0-2.6	0.1-0.4	0.17-0.19
3.0			
Mean	2.21	0.38	0.17
SD	0.86	0.14	0.01
Range	1.4-3.8	0.2-0.6	0.16-0.19
4.5			
Mean	2.64	0.44	0.17
SD	0.81	0.12	0.01
Range	1.4-4.0	0.2-0.7	0.15-0.18
6.0			
Mean	3.56	0.60	0.15
SD	0.39	0.12	0.02
Range	2.9-3.9	0.3-0.7	0.11-0.17
7.5			
Mean	3.53	0.60	0.17
SD	0.81	0.15	0.01
Range	2.6-4.6	0.4-0.8	0.16-0.18
9.0			
Mean	4.11	0.70	0.16
SD	1.77	0.22	0.01
Range	2.3-6.6	0.4-1.0	0.14-0.18
10.5			
Mean	2.70	0.46	0.18
SD	0.64	0.12	0.01
Range	1.9-3.9	0.3-0.8	0.16-0.19
12.0			
Mean	2.56	0.43	0.17
SD	0.61	0.09	0.03
Range	1.9-3.6	0.3-0.6	0.16-0.19

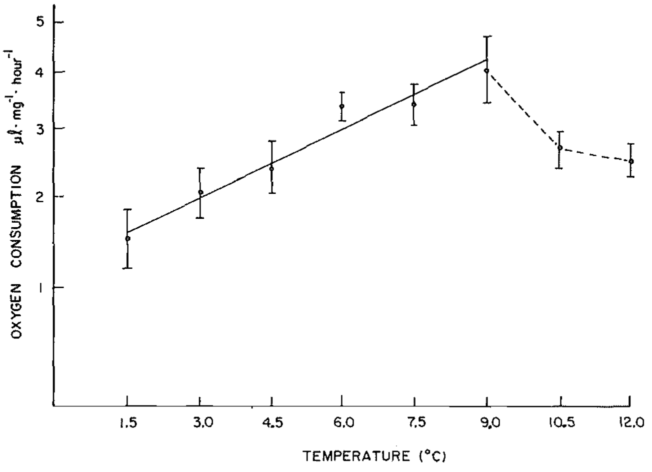


Figure 34.—Oxygen consumption of unfed stage-one larvae of *Pandalus borealis* (from Paul and Nunes 1983).

Temperature and salinity tolerance of larvae and response to currents

In an experiment to determine the upper and lower temperature tolerance limits of larvae, Stickney and Perkins (1980) used a mixed group of 1st to 3rd stage larvae. Exposures were 4 and 22 h, with approximately an hour to reach the test temperature from the acclimation temperature. The acclimation temperatures were 4° and 10°C for upper limit tests, and 4° for lower limit tests. Test temperatures were −1.8°, −1.2°, 14°, 16°, and 18°. After exposure the animals were held for observation at the acclimation temperature for an additional day. Any mortality that occurred during or within a 24-h period after the test exposure was considered to be due to the test conditions. Mortality was negligible at −1.8° and −1.2°C, slight at 14°C. The most serious mortalities resulted from exposures to 16°C or over for an extended period, although even 16° was tolerated by 89% of the 10° acclimated larvae. The results are shown in Table 11.

In addition to acute temperature tolerance tests, a few experiments were also conducted to show the extended effects of temperature and salinity interactions. Third and fourth stage larvae were exposed for 2 wk to 8 different combinations of temperature and salinity, 16 larvae in each combination. The dilutions of seawater were made with demineralized tap water and changed every other day. The larvae were fed *Artemia* nauplii during the experiment. Except for an unusually high mortality of 13% at the eminently salubrious conditions of straight ($31^{0}/_{00}$) seawater at 8°C, the amount of mortality increased with decreasing salinity, and this higher mortality at low salinity was aggravated at lower temperatures (Table 12). This effect is not unusual in decapod crustacea. Mechanisms to regulate osmotic balance in diluted water are geared to respiration and metabolism which is lower at lower temperatures (see Broekema 1942; Flugel 1960).

Stickney and Perkins (1975) conducted preliminary experiments to determine the reaction of juvenile shrimp to directional water currents. Two experimental situations were employed: in one, 25 juvenile shrimp were placed in a rectangular (about 1 m^2) shallow tank, and currents were introduced intermittently by means of a mechanical stirrer. The positions of the test animals in relation to the current or lack of current were recorded hourly. In the other experimental situation, three juveniles were placed in a 3 L beaker (diameter 15 cm) and either a clockwise or a counterclockwise current introduced by means of a water inlet at the top of the beaker. Velocity of the current was approximately 10 cm/s. The current was left on or off for half-hour intervals and the position of the animals then recorded. The animals in the beaker were replaced after three sets of observations.

Table 11.—Tolerance of *Pandalus* larvae to high and low temperature extremes (after Stickney and Perkins 1977).

Acclimation temperature (°C)	Exposure		Number		% Mortality
	Time (h)	Temperature (°C)	Survivors	Dead	
4	3	−1.2	31	1	3
4	22	−1.2	67	1	1.5
4	4	−1.8	20	0	0
4	22	−1.8	40	0	0
4	4	14	20	0	0
4	22	14	23	2	8
4	4	16	14	1	6.7
4	22	16	18	15	45
10	4	16	13	0	0
10	22	16	23	3	11.5
10	22	18	20	6	23

Table 12.—Percent mortality after 2 wk of 2d and 3d stage *Pandalus* larvae exposed to various combinations of temperature and salinity.

Temperature (°C)	Salinity ($^{0}/_{00}$)			
	31.0	27.5	26.0	23.5
8	13	0	11	25
4	6	25	38	38

The juvenile shrimp in both experimental situations showed a marked response, usually facing directly, or nearly directly, away from the current. The summarized results and the chi-square values are given in Table 13. Occasional individuals swimming at the time of observation or perched on the drain pipe were not included in the tallies, hence the differences in total numbers given in the table.

Table 13.—Orientation of shrimp in tank and beaker under four different conditions. Tank = 4 observations of 25 shrimp under each condition; beaker = 22 observations of 3 shrimp under each condition.

	Number facing away from current source	Number facing any other direction	Total
Tank			
Stirrer on	74	20	94
Stirrer off	33	43	76
Total	107	63	170
$\chi^2 = 22.45$			
Beaker			
Current on	56	8	64
Current off	19	46	65
Total	75	54	129
$\chi^2 = 42.63$			

Plankton

Haynes (1983) found the greatest number of planktonic larval *P. borealis* between 20 and 30 m with some diel vertical movement noted. His work was conducted in Kachemak Bay, AK. Perkins (pers. obs.), working in Sheepscot Bay, ME, captured the greatest number of larvae, regardless of stage, at the 20-30 m level also. Water depth in Sheepscot Bay ranged from 48 to 54 m.

Lysy (1981), working in the Norwegian and Barents Seas, found the greatest numbers of larvae between 10 and 25 m at night, while during periods of daylight concentrations occurred between 20 and 50 m.

3.23 Adolescent phases

Stickney and Perkins (1977) found that the onset of external male sexual characteristics was apparent on juvenile shrimp with carapace lengths (CL) of approximately 6 mm. The first indication was a slight protuberance (male copulatory structure) on the endopodites of the first pleopods (Fig. 35). The first noticeable development of the appendix masculina (second pleopods) was evident on animals of 6.5 mm CL (Fig. 36). Cincinnuli (hooklike spines) first normally appear on the male copulatory organ in animals of approximately 8 mm CL. Spinous setae also first appear on the tip of the appendix masculina in animals of 8 mm CL. The cincinnuli of the male copulatory organ are terminally situated when they first appear and then become subterminal in animals of approximately 9.5 mm CL. All normally developing juveniles bore a noticeable indication of the male copulatory structure when they had reached 7 mm CL and all bore at least a rudiment of an appendix masculina. Two juveniles showed

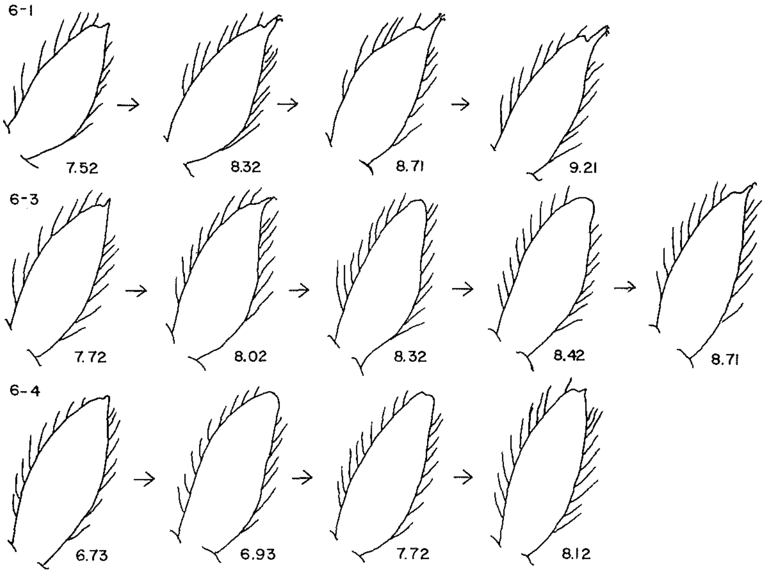


Figure 35.—The endopods of the first pleopod of juvenile shrimp showing the development of the male copulatory organ by successive molts. Each row (indicated by arrows) shows the succession in individual animals. The number at the lower right of each figure indicates the animal's carapace length at that molt. The top row (6-1) of figures indicates normal development (from Stickney and Perkins 1977). Bottom rows indicate abnormal development.

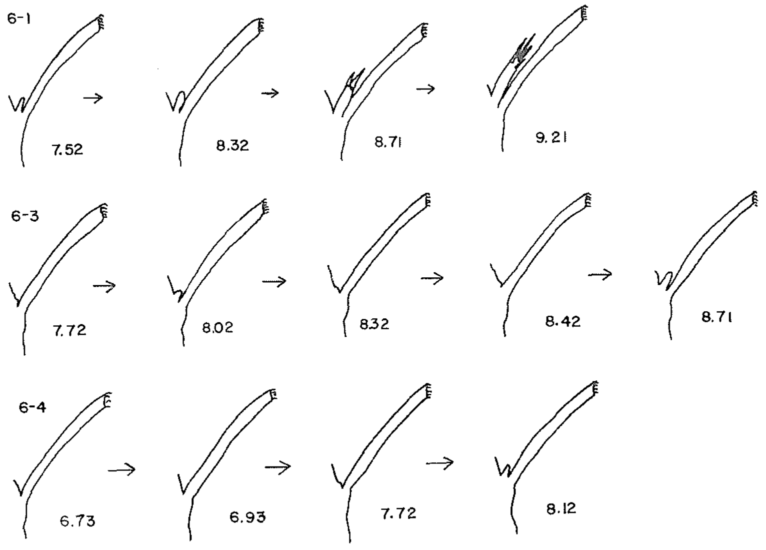


Figure 36.—The appendix interna and the development of the appendix masculina on the second pleopod of juvenile *Pandalus borealis*. These figures correspond to those in the previous figure. The top row (6-1) indicates normal development (from Stickney and Perkins 1977).

definite early signs of development of the external male characteristics then lost any indication of such for two molts, then started developing the characteristics again.

Their observations have definitely established that it is the size of the young shrimp and not its age that determines when external indications of sexual differentiation occur. For example, among juveniles of the same age that were cultured at different temperatures, those that were held at warmer temperatures molted and grew more rapidly than those held at cooler temperatures and thus reached the size at which external sexual characteristics become apparent earlier. Also, within one temperature regime, those individuals that achieved greater size earlier also exhibited the start of external male development earlier.

3.3 Adult phase

3.31 Longevity

The average life expectancy of *P. borealis* varies with geographic region and ranges from 3 (Allen 1959) to 8.5 (Rasmussen 1953) years, though records of specimens over 7.5 yr are rare (see Table 14). Skuladottir (1981a) reported ages up to 11.8 yr using her deviation method.

3.32 Hardiness

Pandalus borealis have been maintained in the laboratory for extended periods with no difficulty. Stickney and Perkins (unpubl. data) maintained the shrimp through the ovigerous period and at least three molts. Survival was approximately 80%. The shrimp appear to be relatively hardy. Specimens have been collected with an otter trawl, and maintained in seawater-filled coolers before transport to the laboratory with no apparent ill effects (Stickney and Perkins, unpubl. data).

3.33 Competitors

Pandalus borealis is an important member of the deep water ecosystem and functions as both predator and prey. There are few records of specific competitor species (*Pandalus montagui* and

Table 14.—Maximum age or approximate age at last breeding (years) for *Pandalus borealis*.

Age (yr)	Locality	Reference
3	Northumberland, U.K.	Allen (1959)
4	British Columbia	Berkeley (1930)
4	British Columbia	Butler (1964)
4	Japan Sea	Ito (1976)
4	Oslo Fjord, Norway	Rasmussen (1953)
5	Gulf of Maine	Haynes and Wigley (1969) Apollonio and Dunton (1969)
5-6	Kachemak Bay, AK	Barr (1970b)
6	Thomas Bay, AK	McCrary (unpublished—quoted in Charnov 1979)
6	Mist Fjord, Norway	Rasmussen (1953)
6.5	Hopen Island, Barents Sea	Bryazgin (1967)
6+		Ivanov (1969a)
7	Kiluda Bay, Ugak Bay, Two-headed Island, AK	Fox (1972)
7	Western Gulf of Alaska	Ivanov (1969b)
7	Bering Sea	Ivanov (1969b)
7+	Japan Sea	Kurata (1981)
>7.5	Spitsbergen	Rasmussen (1953)

Eualus macilentus: Bigelow and Schroeder 1939; Squires 1961, 1970), although it is not unreasonable to assume that there are several others amongst the more commonly occurring sympatric species. A listing of associated species is given in Table 15.

3.34 Predators

The pink shrimp plays a major role as food for fish stocks and has been listed as a major food item for the following species.

Atheresthes stomias	Mito (1974); Smith et al. (1976)
Gadus callarias (*G. morhua*)	Horsed and Smidt (1956); Smidt (1967); Howard (1980)
G. macrocephalus	Jewett (1978); Rogers et al. (1979)
Gadus sp.	Stephensen (1939)
Hippoglossoides elassodon	Rogers et al. (1979)
Hypoglossus stenolepsis	Best (1979)[5]; Novikov (1968)
Limanda aspera	Rogers et al. (1979)
Lycodes seminudus	Horsted and Smidt (1956)
L. vahlii	Horsted and Smidt (1956)
Merluccius bilinearis	Squires (1961, 1970); Bigelow and Schroeder (1939)
Myxine glutinosa	Shelton (1978)
Reinhardtius hippoglossoides	Bigelow and Schroeder (1939); Horsted and Smidt (1956); Squires (1961, 1965); Bowering and Parsons (1981)
Sebastes marinus	Horsted and Smidt (1956)
Theragra chalcogramma	Takahashi and Yamaguchi (1972); Smith et al. (1976)

In addition, the species provides a food source for harbor seals and octopuses (Barr 1970b) and undoubtedly for many other species of fishes commonly encountered with *P. borealis* (see Table 15).

3.35 Parasites, diseases, injuries, and abnormalities

There have been several reports of parasites occurring on *P. borealis*, the most common being the bopyrid isopods *Bopyroides hyppolytes* (branchial cavity) and *Hemiarthrus* (*Phryxus*) *abdominalis* (ventral surface of abdomen) (Hjort and Ruud 1938; Horsted and Smidt 1956; Richardson 1905; Warren 1974; and Uzmann 1967[6]). Horsted and Smidt (1965) reported *H. abdominalis* on male individuals only and suggested that their presence hindered development and molting such that sex reversal did not take place. Berruer-Bonnenfant and Charniaux-Cotton (1965) reported that infestation of *P. borealis* by *H. abdominalis* leads to feminization of the male shrimp. They noted that parasitized *P. borealis* showed secondary sexual characteristics resembling those of a transitional individual in that the copulatory organ and the appendix masculina were in regression. They also found that the gonad appeared as a transitional gonad and attributed the feminization to a depletion of hormone levels. Warren (1974) reported *H. abdominalis* in shrimp < 23 mm CL. Appollonio and Dunton (1969) reported infestation of the gill lamellae by an epizoic protozoan *Gymnodinoides* spp.; however, a disease called black spot syndrome was later reported by Rinaldo and Yevich (1974) but the protozoan was not the causative organism. Black spot is characterized by tissue destruction of the gill lamellae and vacuolated chitin growth over the damaged tissue which produces macroscopic black spots on the gills. Further, it occurs in cyclic fashion and peaks in late fall and winter in the Gulf of Maine (Apollonio and Dunton 1969; Rinaldo and Yevich 1974).

Other reported parasites include the rhyzocephalan *Sylon hippolytes* (Butler 1980), a single incidence of infestation by the nematode *Thynnascaris* (*Contracaecum*) sp. (Margolis and Butler 1954), and a flagellated protozoan parasite in the shrimp eggs which causes egg-death (Stickney 1978) (Fig. 37). Butler (1980) also reported infection of *P. borealis* with microsporidia.

3.36 Chemical composition

There have been few studies concerned with the chemical composition of *P. borealis*. Table 16 summarizes the fatty acid composition of both berried and nonberried shrimp as determined by Ackman and Eaton (1967). In a further experiment they reported 0.83% lipid recovery composed of 47% phospholipid, 43% triglyceride, and 10% sterol with a small amount of diglyceride. There were no free fatty acids or sterol esters and pigment was estimated at < 0.1%. They also noted a high iodine level. In the absence of significant amounts of carbohydrates, lipid has been identified as the main energy reserve in *P. borealis* (Bamstedt 1974).

Hopkins (1979) presented a preliminary study of body composition in 4 year classes and in the eggs of *P. borealis* and these data are summarized in Table 17.

More recently, Seiring and Hopkins (in press) studied the effects of starvation on body weight and composition in *P. borealis*. They concluded that prawns of different ages use different methods for coping with starvation stress. Small individuals decreased their weight specific oxygen consumption rates more so than the larger prawns, carbon and lipid both showed a greater decrease in young prawns than in old ones; however, there was no

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[5] Best, E. A. 1979. Halibut ecology. *In* Fisheries oceanography - eastern Bering Sea shelf. p. 127-165. Northwest and Alaska Fisheries Center Processed Rep. 79-20.

[6] J. R. Uzmann, personal communication *in* Sindermann, C. J., and A. Rosenfield. 1967. Principal diseases of commercially important marine bivalve mollusca and crustacea. U.S. Fish Wildl. Serv., Fish. Bull. 66:335-385.

Table 15.—Species associated with the northern shrimp *Pandalus borealis*.

Species	Source
COELENTERATES	
Bolocera longicornis	Hjort and Ruud (1938)
Periphylla hyacinthina	Horsted and Smidt (1956)
Plychogen lactea	Horsted and Smidt (1956)
POLYCHAETES	
Glycera rouxi	Allen (1959)
MOLLUSCS	
Abra nitida	Allen (1959)
Arca glacialis	Horsted and Smidt (1956)
Astarte crenata	Horsted and Smidt (1956)
A. elliptica	Horsted and Smidt (1956)
Buccinum hydrophanum	Horsted and Smidt (1956)
B. tenue	Horsted and Smidt (1956)
B. terra-novae	Horsted and Smidt (1956)
B. undatum	Horsted and Smidt (1956)
B. undulatum	Horsted and Smidt (1956)
Cardium ciliatum	Horsted and Smidt (1956)
Chlamys septemradiatus	Hjort and Ruud (1938)
Cuspidaria obesia	Horsted and Smidt (1956)
Dendronotus robustus	Horsted and Smidt (1956)
Funiculina quadrangularis	Hjort and Ruud (1938)
Gonatus fabricii	Horsted and Smidt (1956)
Leda minula	Horsted and Smidt (1956)
L. pernula	Horsted and Smidt (1956)
Lepeta coeca	Horsted and Smidt (1956)
Moschites cirrosa	Hjort and Ruud (1938)
Neptunea despecta	Horsted and Smidt (1956)
Nucula tenuis	Horsted and Smidt (1956)
Onchidiopsis groenlandica	Horsted and Smidt (1956)
Pecten islandicus	Horsted and Smidt (1956)
Polypos articus	Hjort and Ruud (1938)
Portlandia lenticula	Horsted and Smidt (1956)
Psammobia ferroensis	Horsted and Smidt (1956)
Rossia leucopis	Bigelow and Schroeder (1939), Squires (1961, 1970)
R. sp.	Horsted and Smidt (1956)
R. macrusoma	Hjort and Ruud (1938)
Sepiola rondellette	Hjort and Ruud (1938)
Serripes groenlandicum	Horsted and Smidt (1956)
Sipho togatus	Horsted and Smidt (1956)
Stichopus tremulus	Hjort and Ruud (1938)
Thyasira flexuosa	Allen (1959), Broch (1935), Horsted and Smidt (1956)
Yoldia thraciaeformis	Horsted and Smidt (1956)
CRUSTACEANS	
Acanthostepheia malmgreni	Horsted and Smidt (1956)
Argis spp.	Ippolito (1980)
Boreomysis arctica	Hjort and Ruud (1938)
B. nobilis	Horsted and Smidt (1956)
Calocaris macandreae	Hjort and Ruud (1938), Rathbun (1883)
Cancer borealis	Stickney and Perkins (unpubl. data)
C. irroratus	Stickney and Perkins (unpubl. data)
Caridion sp.	Stickney and Perkins (unpubl. data)
Chionoecetes opilio	Horsted and Smidt (1956)
Crangon allmani	Allen (1959), Hjort and Ruud (1938)
C. septemspinosa	Stickney and Perkins (unpubl. data)
Dichelopandalus leptocerus	Rathbun (1883), Clark (1982)
Eualus fabricii	Stickney and Perkins (unpubl. data)
E. gaimardii	Stickney and Perkins (unpubl. data)
E. pusiolus	Stickney and Perkins (unpubl. data)
Eupagurus pubescens	Hjort and Ruud (1938), Horsted and Smidt (1956)
Euphausiacea sp. sp.	Horsted and Smidt (1956)
Eusirus holmii	Horsted and Smidt (1956)
Gammarus oceanicus	Horsted and Smidt (1956)
Geryon sp.	Bigelow and Schroeder (1939)
Hyas coarctatus	Horsted and Smidt (1956)
Lebbeus groenlandicus	Stickney and Perkins (unpubl. data)
L. polaris	Stickney and Perkins (unpubl. data)
L. zebra	Stickney and Perkins (unpubl. data)
Lithodes maja	Hjort and Ruud (1938), Horsted and Smidt (1956)
Lophogaster typicus	Hjort and Ruud (1938)
Meganyctiphanes norvegica	Hjort and Ruud (1938)
Munida sarsi	Hjort and Ruud (1938)

Table 15.—*Continued.*

Species	Source
Munidopsis curvirostra	Horsted and Smidt (1956)
Nectocrangon lar	Horsted and Smidt (1956)
Nephrops norvegicus	Hjort and Ruud (1938), Rathbun (1883)
Pagurus spp.	Stickney and Perkins (unpubl. data)
Pandalopsis dispar	Ippolito (1980), Harry (1964)
P. japonica	Kurata (1981)
P. ochotensis	Kurata (1981)
Pandalidae spp.	Hjort and Ruud (1938), Ippolito (1980)
Pandalus borealis	Horsted and Smidt (1956), Hjort and Ruud (1938), Ippolito (1980)
P. brevirostris	Hjort and Ruud (1938)
P. goniurus	Ippolito (1980), Harry (1964)
P. hypsinotus	Harry (1964), Kurata (1981), Ippolito (1980)
P. kessleri	Kurata (1981)
P. montagui	Rathbun (1883), Clark (1982), Hjort and Ruud (1938), Horsted and Smidt (1956)
P. platyceros	Ippolito (1980)
P. propinguus	Bigelow and Schroeder (1939), Hjort and Ruud (1938)
Pasiphaea sivado	Hjort and Ruud (1938)
P. tarda	Horsted and Smidt (1956), Hjort and Ruud (1938)
Phryxus adominalis	Horsted and Smidt (1956)
Pontophilus norvegicus	Hjort and Ruud (1938), Horsted and Smidt (1956)
Portunus depurator	Hjort and Ruud (1938)
P. holsatus	Hjort and Ruud (1938)
Sabinea septemcarinata	Horsted and Smidt (1956)
Sclerocrangon boreas	Horsted and Smidt (1956)
Spirontocaris gaimardii	Horsted and Smidt (1956)
S. lilljeborgii	Rathbun (1883), Hjort and Ruud (1938)
S. machilenta	Horsted and Smidt (1956)
S. phippsii	Stickney and Perkins (unpubl. data)
S. polaris	Horsted and Smidt (1956), Hjort and Ruud (1938)
S. sp.	Ippolito (1980)
S. spinus	Stickney and Perkins (unpubl. data)
Sergestes articus	Horsted and Smidt (1956)
ECHINODERMS	
Amphiura chiajei	Allen (1959)
A. sp.	Horsted and Smidt (1956)
Antoptilum grandiflorum	Horsted and Smidt (1956)
Asteronyx loveni	Hjort and Ruud (1938)
Ctenodiscus crispatus	Horsted and Smidt (1956)
Heliometra glacialis	Horsted and Smidt (1956)
Henricia sanguinolenta	Horsted and Smidt (1956)
Hippasteria phrygiana	Horsted and Smidt (1956)
Leptasterias polaris	Horsted and Smidt (1956)
Odinia semicoronata	Horsted and Smidt (1956)
Ophiacantha bidentata	Horsted and Smidt (1956)
Ophiopholis aculeala	Horsted and Smidt (1956)
Ophiura sarsi	Horsted and Smidt (1956)
Solaster endeca	Horsted and Smidt (1956)
Solaster papposus	Horsted and Smidt (1956)
Stephanasterias albula	Horsted and Smidt (1956)
Strongylocentrotus drobachiensis	Horsted and Smidt (1956)
Urasterias linckii	Horsted and Smidt (1956)
FISHES	
Agonus acipenserinus	Ippolito (1980)
Anarhichus minor	Horsted and Smidt (1956)
A. lupus	Horsted and Smidt (1956)
A. latifrons	Horsted and Smidt (1956)
Anoplopoma fimbria	Ippolito (1980)
Aptocyclus ventricosus	Ippolito (1980)
Argentina silus	Hjort and Ruud (1938)
A. sphyraena	Hjort and Ruud (1938)
Artediellus uncinatus	Horsted and Smidt (1956), Bigelow and Schroeder (1939)
Aspidophoroides monoplerygius	Horsted and Smidt (1956)
Atheresthes stomias	Ippolito (1980)
Bathylagus benedicti	Horsted and Smidt (1956)
Bathymaster signatus	Ippolito (1980)
Boreogadus saida	Horsted and Smidt (1956)
Brosme brosme	Bigelow and Schroeder (1939), Horsted and Smidt (1956)
Callionymus lyra	Hjort and Ruud (1938)
Careproctus reinhardti	Horsted and Smidt (1956)
Centroscyllium fabricii	Horsted and Smidt (1956)
Chimaera monstrosa	Hjort and Ruud (1938)

Table 15.—*Continued.*

Species	Source
Clupea harengus	Bigelow and Schroeder (1939), Fontaine and Paturel (1972), Hjort and Ruud (1938)
C. harengus pallasi	Ippolito (1980)
C. sprattus	Hjort and Ruud (1938)
Cottus scorpius	Horsted and Smidt (1956)
Cryptacanthodes maculatus	Bigelow and Schroeder (1939)
Cyclopterus lumpus	Bigelow and Schroeder (1939)
Dasycottus setiger	Ippolito (1980)
Drepanopsetta platessoides	Hjort and Ruud (1938)
Enchelyopus cimbrius	Bigelow and Schroeder (1939)
Etmopterus spinax	Hjort and Ruud (1938)
Eumicrotremus spinosus	Horsted and Smidt (1956)
Gadiculus thori	Hjort and Ruud (1938)
Gadus aeglefinus	Hjort and Ruud (1938), Horsted and Smidt (1956)
G. esmarki	Hjort and Ruud (1938)
G. macrocephalus	Ippolito (1980)
G. merlangus	Hjort and Ruud (1938)
G. minutus	Hjort and Ruud (1938)
G. morhua	Hjort and Ruud (1938), Fontaine and Paturel (1972), Horsted and Smidt (1956)
G. ogac	Horsted and Smidt (1956)
G. pollachius	Hjort and Ruud (1938)
G. poutassou	Hjort and Ruud (1938)
Gaidropsarus argentatus	Bigelow and Schroeder (1939)
Glyptocephalus cynoglossus	Bigelow and Schroeder (1939), Fontaine and Paturel (1972), Horsted and Smidt (1956)
G. zachirus	Ippolito (1980)
Gymnacanthus tricuspis	Horsted and Smidt (1956)
Hemilepidotus spinosus	Ippolito (1980)
H. hemilipidotus	Ippolito (1980)
H. jordani	Ippolito (1980)
Hexagrammus decagrammus	Ippolito (1980)
Hippoglossoides elassodon	Ippolito (1980)
H. platessoides	Bigelow and Schroeder (1939), Fontaine and Paturel (1972), Horsted and Smidt (1956)
Hyppoglossus stenolepsis	Ippolito (1980)
Icelus bicornis	Horsted and Smidt (1956)
Isopsetta isolepsis	Ippolito (1980)
Lampanyctus crocodilus	Horsted and Smidt (1956)
Lepidopsetta bilineata	Ippolito (1980)
Leptagonus decagonus	Horsted and Smidt (1956)
Limanda aspera	Ippolito (1980)
Liparis dennyi	Ippolito (1980)
Liparis sp.	Horsted and Smidt (1956)
Lophius americanus	Bigelow and Schroeder (1939), Fontaine and Paturel (1972)
L. piscatorius	Hjort and Ruud (1938)
Lumpenella longirostris	Ippolito (1980)
Lumpenus sagitta	Ippolito (1980)
L. maculatus	Horsted and Smidt (1956)
L. lampetriformis	Hjort and Ruud (1938), Horsted and Smidt (1956)
Lycodes agnostus	Horsted and Smidt (1956)
L. brevipes	Ippolito (1980)
L. eudipleurostictus	Horsted and Smidt (1956)
L. nigricans	Horsted and Smidt (1956)
L. palearis	Ippolito (1980)
L. seminudus	Horsted and Smidt (1956)
L. vahli	Horsted and Smidt (1956), Hjort and Ruud (1938)
Lycenchelys sarsi	Hjort and Ruud (1938)
Macrurus bairdii	Bieglow and Schroeder (1939)
M. fabricii	Horsted and Smidt (1956)
M. rupestris	Hjort and Ruud (1938)
Mallotus villosus	Ippolito (1980), Horsted and Smidt (1956)
Microgadus proximus	Ippolito (1980)
Microstomus pacificus	Ippolito (1980)
Molva byrkelange	Horsted and Smidt (1956)
Myctophum glaciale	Horsted and Smidt (1956)
Myxine glutinosa	Bigelow and Schroeder (1939), Hjort and Ruud (1938)
Myoxocephalus sp.	Ippolito (1980)
M. polyacanthocephalus	Ippolito (1980)
Oncorhynchus tshawytscha	Ippolito (1980)
Onos cimbrius	Hjort and Ruud (1938)
Osmerus mordax dentax	Ippolito (1980)
Paralepis rissoi kroyeri	Horsted and Smidt (1956)
Parophrys vetulus	Ippolito (1980)
Platichthys stellatus	Ippolito (1980)

Table 15.—*Continued.*

Species	Source
Pleuronectes cynoglossus	Hjort and Ruud (1938)
P. microcephalus	Hjort and Ruud (1938)
P. platessa	Hjort and Ruud (1938)
Pollachius virens	Fontaine and Paturel (1972), Bigelow and Schroeder (1939)
Psettichthys melanostictus	Ippolito (1980)
Raia scabrata	Bigelow and Schroeder (1939)
R. senta	Bigelow and Schroeder (1939)
R. stabuliforis	Bigelow and Schroeder (1939)
Raja clavata	Hjort and Ruud (1938)
R. nidarosiensis	Hjort and Ruud (1938)
R. radiata	Hjort and Ruud (1938), Horsted and Smidt (1956), Fontaine and Paturel (1972)
Reinhardtius hipploglossoides	Ippolito (1980), Horsted and Smidt (1956)
Rhombus maximus	Hjort and Ruud (1938)
Ronquilus jordani	Ippolito (1980)
Sebastes marinus	Bigelow and Schroeder (1939), Fontaine and Paturel (1972), Hjort and Ruud (1938)
S. melanops	Ippolito (1980)
S. ciliatus	Ippolito (1980)
S. flavidus	Ippolito (1980)
S. alutus	Ippolito (1980)
Stomias boa ferox	Horsted and Smidt (1956)
Squalus acanthias	Bigelow and Schroeder (1939), Hjort and Ruud (1938)
Thaleichthys pacificus	Ippolito (1980)
Theragra chalcogramma	Ippolito (1980)
Trichodon trichodon	Ippolito (1980)
Trigla gurnardus	Hjort and Ruud (1938)
Triglops sp.	Horsted and Smidt (1956)
Urophycis chesteri	Fontaine and Paturel (1972), Bigelow and Schroeder (1939)
U. chuss	Fontaine and Paturel (1972), Bigelow and Schroeder (1939)
U. tenuis	Bigelow and Schroeder (1939)

clear relationship between the changes in nitrogen and protein levels.

3.4 Nutrition and growth

3.41 Feeding

Pandalus borealis can best be described as an opportunistic omnivore functioning as both a predator and a scavenger (Barr 1970b; Butler 1964; Dahlstrom 1970; Feder et al. 1978; Fox 1972; Mistakidis 1957). While the species is predominantly a benthic feeder, it is known to feed in the water column during diel vertical migrations (Wollebaek 1903; Barr 1970a) (see section 2.22).

In addition, feeding patterns have been shown to vary with season, geographic location, and reproductive cycle (Apollonio and Dunton 1969).

There are no specific accounts of the feeding mechanisms employed by *P. borealis*.

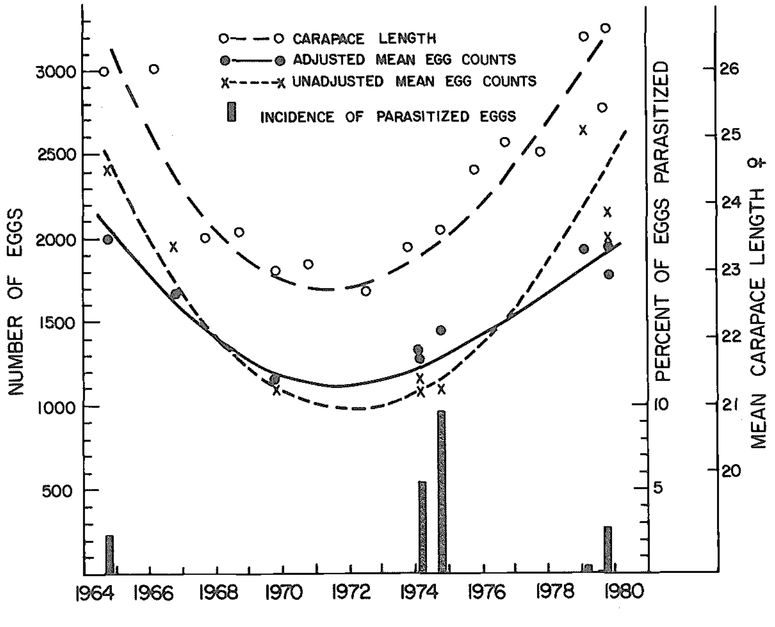

Figure 37.—Adjusted mean egg numbers for samples of shrimp taken for the 1964, 1966, 1969, 1973, 1974, 1978, and 1979 egg year classes. Means adjusted to a standard carapace length of 25 mm. Vertical bars and right hand scale represent mean percentages of egg mass killed by parasitic infection. Also shown are mean carapace lengths of female shrimp (open circles) and unadjusted egg counts (x's) (from Stickney text footnote 4).

Table 16.—Composition of total fatty acids of *Pandalus borealis* in weight percent, by type of acid (from Ackman and Eaton 1967).

Fatty acid	Sample A (nonberried)	Sample B (berried)
Saturated		
12:0	0.3	0.3
14:0	2.9	2.8
15:0	0.5	0.6
16:0	14.9	14.3
17:0	0.3	0.5
18:0	2.6	1.8
19:0	NSA[1]	NSA
20:0	Trace[1]	Trace
Σ	21.5	20.3
Monounsaturated[2]		
14:1	0.5	0.3
15:1	0.4	0.2
16:1	14.1	14.0
17:1	0.4	0.9
18:1	20.2	19.7
19:1	0.2	0.3
20:1	4.8	3.8
22:1	4.9	4.3
24:1	0.3	0.2
Σ	45.8	43.7
Polyunsaturated		
16:2ω4	0.5	0.5
16:3ω4	0.4	0.3
16:4ω1	0.4	0.5
18:2ω6	0.8	1.0
18:3ω6	0.4	0.5
18:3ω3	0.6	0.8
18:4ω3	0.9	1.0
20:2ω6	0.2	0.4
20:3ω6	NSA	NSA
20:4ω6	1.3	1.7
20:4ω3	0.7	0.7
20:5ω3	15.3	17.4
21:5ω2	0.5	0.6
22:2ω6	0.1	0.2
22:4ω6	0.4	0.3
22:5ω6	0.3	0.2
22:5ω3	0.9	1.3
22:6ω3	8.9	8.6
Σ	32.6	36.0

[1] NSA = no significant amount.

[2] The ω9 isomers should predominate, but others may be present.

3.42 Food

Table 18 summarizes the reported food items for *P. borealis* and it is clear that the species is opportunistic in its feeding habits. Cannibalism has been noted by Hansen and Hermann (1953) and Allen (1959). In the most elaborate and detailed study of feeding in the pink shrimp, Weinberg (1981) (see Table 19) concluded that the spectrum of food organisms is determined essentially by the prey available, the time of day, and the developmental stage of the shrimp. He noted that females appear to cease feeding prior to premolt periods; animals with full ovaries showed relatively low nutrient intake. He also demonstrated a diurnal feeding pattern for all sexual stages with maximum stomach fullness occurring in the early afternoon. He further showed that two-thirds of the specimens examined contained sand or small stones which function as a gastric mill (lacking in the Pandalidae).

Table 17.—Mean variations in body weight and body content for 1977, 1976, 1975, and 1974 year-classes of *Pandalus borealis* and egg masses from 1974 year class. Specimens collected 9 February 1978. Weights, percentages, and caloric values are expressed as g, dry body weight, and ash-free dry weight, respectively (condensed from Hopkins 1979).

	1977 (8 mm)	1976 (15 mm)	1975 (19 mm)	1974 (22 mm)	Egg mass (22 mm)
Wet weight	0.440	2.753	5.348	8.043	1.379
Dry weight	0.063	0.589	1.271	1.943	0.064
Protein percent	37.02	41.14	39.25	50.05	25.26
Protein weight	0.024	0.239	0.504	0.975	0.021
Lipid percent	16.9	28.4	26.88	28.08	17.78
Lipid weight	0.010	0.165	0.342	0.544	0.015
Carbon percent	48.21	46.37	45.19	44.22	41.99
Carbon weight	0.030	0.281	0.573	0.860	0.027
Nitrogen percent	10.45	9.59	9.62	9.29	8.48
Nitrogen weight	0.007	0.058	0.121	0.174	0.006
Ash percent	31.26	17.89	18.05	19.53	20.90
Ash weight	0.020	0.104	0.228	0.379	0.014
KCal/g	4.027	5.810	5.625	5.467	5.548
Total KCal	0.252	3.411	7.143	10.616	0.358
Water weight	0.377	2.164	4.077	6.100	1.315
Wet/dry	7.100	4.720	4.220	4.148	34.740
Carbon/nitrogen	4.698	4.900	4.796	4.778	4.958
Lipid/protein	0.513	0.692	0.732	0.545	0.734

3.43 Growth and morphometry

Shrimp lack a suitable structure with which to determine age and, consequently, age estimates and growth rates have been made using length-frequency data. This method presents some difficulties for a species since there is considerable overlap amongst the larger size classes, unless care is taken to distinguish between developmental stages. Skuladottir (1981a) presented a method for detecting year-classes of *P. borealis* from length distributions with relative simplicity. Her method is a modified version of Sund (1930) and is based on the deviations formed when length-frequency distributions are subtracted from a mean length-frequency distribution of several years. Her method involves no complicated calculations and the data seem to fit the von Bertalanffy growth equation to some degree. The only drawback of her method seems to be that only data on one cohort can be compiled.

Previous studies have shown that growth rates in *P. borealis* vary according to region and also between sexes and age classes. Figure 38 shows the growth curves for populations of *P. borealis* from various parts of its range and it can be seen that in general, populations in subarctic waters (Jan Mayen and Spitsbergen) develop more slowly and have a longer life span than those from warmer, more boreal waters (e.g., Gulf of Maine).

Berkeley (1930) first studied growth in *P. borealis*. She demonstrated a general pattern of seasonal growth (see Fig. 39). Rapid growth takes place during the first summer, slows during the winter, and resumes at a rapid pace in the second spring and summer when the growth of males is again slowed. Growth in transitionals is also rapid until sex change takes place at which time growth virtually ceases. The same trends were found by Haynes and Wigley (1969) for *P. borealis* in the Gulf of Maine (Table 20).

The length-weight relationship of *P. borealis* has also been shown to vary between sexes (Table 21). Apollonio and Dunton (1969) reported the relation of length to live weights in *P. borealis* from the Gulf of Maine as: $\text{Log } Y = -0.70502 + 0.06147\ X$ and Howard (1977a) gave a conversion for meat weight to whole weight of $W_{\text{meat}} = 0.48\ W_{\text{whole}}$

Table 18.—Food items reported for adult *Pandalus borealis*.

Locality	Food items	References
Norway	Remains of polychaetes, holothuroidea, porifera, copepoda, radiolarians, diatoms, foraminiferans, peridineans, green algae, tintinnoids, mud	Wollebaek (1903)
Norway	Polychaetes, holothuroids, porifera, copepods, radiolaria, foraminifera, diatoms, peridineans	Hjort and Ruud (1938)
Greenland	Mysids, polychaetes, foraminifera, radiolaria, sand, planktonic crustaceans	Horsted and Smidt (1956)
	Phytobenthos (gammarid amphipods), crustaceans, polychaetes, foraminifera, pelecypods, ophiuroids, euphausiids, copepods	Squires (1970)
Northumberland, United Kingdom	Bottom microfauna, plankton, foraminiferans, small crustaceans, *P. borealis* and *P. montagui* larvae, polychaetes	Allen (1959)
Alaska	Amorphous detritus organic matter and macro algae (*Fucus*, *Porphyra*, *Ulva*, *Bangia*), shrimp, copepods, crabs, tiny clams; 26 species of diatoms representing mud flat, epiphytic and planktonic forms	Crow (1977)
Alaska	Diatoms, plants, foraminifera, porifera, coelenterates, nematodes, polychaeta, gastropoda, bivalvia, crustaceans, echinoderms, chaetognatha, teleostei, sediment	Rice et al. (1979)[1]
Japan	Crustaceans, bivalves, ophiuroids, annelids, fish scales, mud, sand	Kurata (1957)

[1] Rice, R. L., K. I. McCumby, and H. M. Feder. 1979. Food of *Pandalus borealis*, *Pandalus hypsinotus* and *Pandalus goniurus* (Pandalidae, Decapoda) from Tower Cook Inlet, Alaska. Unpubl. manuscr., 15 p. Institute of Marine Sciences, University of Alaska, Fairbanks, Seward, AK 99664.

The conversion factor, defined as the relative length of the carapace to the total length (tip of rostrum to tip of telson), varies indirectly with size increase (Table 22). In the closely related species, *P. platyceros*, the decrease in the value of the conversion factor has been attributed to the difference in rostral growth rates after sex reversal (Butler 1970).

3.44 Metabolism

Metabolism in adult *P. borealis* has been studied by several authors (Johnson 1936; Fox 1936, 1939; Fox and Winfield 1937; van Heerdt and Krijgsman 1939; Abercrombie and Johnson 1941; Wolvekamp and Waterman 1960). Fox (1936) reported a mean $\dot{V}O_2$ of 102 µL/g wet weight per h at 10°C and 75 µL/g wet weight per h at 6.5°C. He also reported heart rates of 63, 86, and 126 beats/min and scaphognathite beats of 126, 160, and 209 beats/min at 3.5°, 6.5°, and 11°C, respectively. Fox and Winfield

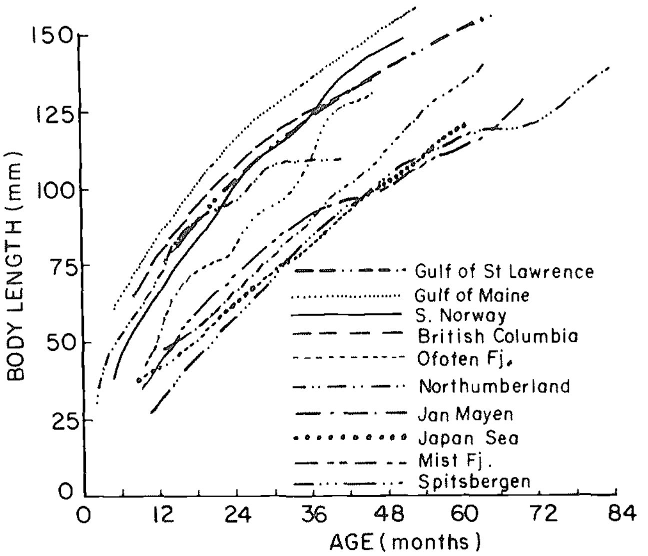

Figure 38.—Growth curves of 10 populations of *Pandalus borealis* (data from Rasmussen 1953; Allen 1959; Haynes and Wigley 1969; Ivanov 1969b; Butler 1971; Simard et al. 1975; Ito 1976).

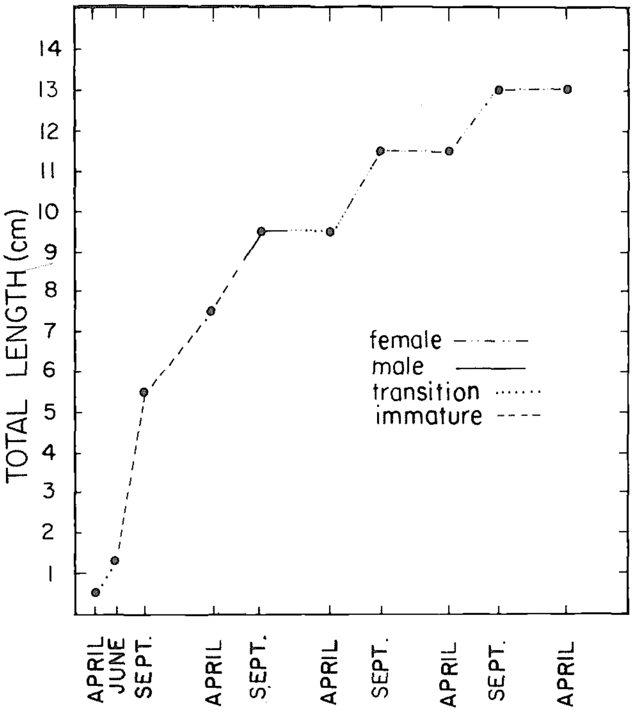

Figure 39.—Rate of growth and phases of development of *Pandalus borealis* (after Berkeley 1930).

Table 19.—Particles and prey identified among the stomach contents of 1,147 deep sea shrimp, *Pandalus borealis*. *N* is the number of prey specimens of each species that were identified. In the cases of "Other items" and "Unidentified," the number of *Pandalus* specimens containing these items is given. cf, with a specific identification, means the genus is established without doubt; otherwise it means uncertain. (From Weinberg 1981.)

	N		*N*
NEMATODES	4	Harpacticoidea	17
NEMERTINI	1cf	Copepoda parasitica	
MOLLUSCA (total)	58	*Caligus* cf. *rapax*	1
Gastropoda		Cirripedia, larvae	1
Lunatia sp.	35	Amphipoda (total)	13
Lamellibranchiata		*Arrhis* sp.	2cf
Cardium minimum	3	*Haploops tubicola*	1
Venus fasciata	1	*Harpinia* sp.	2
Spisula sp.	1	*Harpinia antennaria*	1
Cephalopoda	3	*Ampelisca* sp.	1
Mollusca indet.	15	*Ampelisca macrocephala*	1
POLYCHAETA (total)	133	Amphipoda indet.	5
Errantia		Isopoda	
Paramphinome jeffreysii	25	*Gnathia* sp.	1
Harmothoe nodosa	2	Tanaidacea	
Harmothoinae	2	*Typhlotanais* sp.	4
Pholoe minuta	1	Euphausiacea (total)	39 + 4cf
Anaitides groenlandica	1	*Thysanoessa inermis*	6 + 3cf
Phyllodocidae	1	*Nyctiphanes couchi*	1
Syllidae	1	*Meganyctiphanes norvegica*	3
Nephtys sp.	3	Mysidacea (total)	6
Sphaerodorum flavum	1	*Leptomysis gracilis*	1
Glycera rouxii	4 + 1cf	Mysidacea indet.	5
Lumbrinereis sp.	2cf	Cumacea (total)	6
Sedentaria		*Eudorella* sp.	1
Spiochaetopterus typicus	1	*Eudorella emarginata*	3
Diplocirrus glaucus	1	*Leucon* cf. *nasica*	1
Ophelina acuminata	1cf	*Leptostylus villosus*	1
Capitellidae	2 + 1cf	Decapoda (total)	9 + 2cf
Praxillella sp.	1	*Cancer pagurus*, Megalopa	1
Pectinaria sp.	4	*Pandalus borealis*, juv.	1 + 1cf
Ampharete sp.	1	Decapoda, larvae	2 + 1cf
Streblosoma bairdi	1	Decapoda, indet.	2 + 2cf
Terebellides stroemi	1	Crustacea indet.	84
Polychaeta indet.	71	ECHINODERMATA (total)	22 + 2cf
ACARI	2	Echinoidea	4
CRUSTACEA (total)	209	Ophiuroidea	9 + 2cf
Ostracoda	6	Asteroidea	9
Copepoda nonparasitica (total)	32	CHAETOGNATHA	1
		PISCES	8
OTHER ITEMS		UNIDENTIFIED	
"Detritus"	804	Chitinous shreds	283
Small stones, sand grains	764	Oil droplets	117
Bristles, needles, spines	517	Fibers	65
Shell fragments	426	Fleshy remains	42
Scales of *Boreogadus esmarkii*	237	Teeth	13
Foraminiferans	53	Eggs and cysts	2

Table 20.—Summary of the size, by age and sex, of northern shrimp from the Gulf of Maine (from Haynes and Wigley 1969).

Month	Age (mo)	Sex	Mean carapace length (mm)	Mean total length (mm)	Mean total weight (g)
Oct.	6	Male	8.1	45.7	0.3
Feb.	10	Male	11.2	63.2	0.9
June	14	Male	14.0	79.0	1.7
Oct.	18	Male	16.7	94.2	2.8
Feb.	22	Male	19.0	107.2	4.1
June	26	Male	20.8	117.3	5.4
Oct.	30	Male	22.4	126.3	6.8
Feb.	34	Transitional	23.8	134.2	8.1
June	38	Transitional	24.9	140.4	9.4
Oct.	42	Female	25.8	145.5	11.9
Feb.	46	Female	26.6	150.0	13.0

Table 21.—Equations relating log weight to log carapace length for *Pandalus borealis*.

Equation	Forms included[1]	Area	Reference
$\mathrm{Log}\ W = -2.578 + 2.551\ \mathrm{Log}\ L$	♀ ♂ ⚥	Aberdeen, U.K.	Howard (1977b)
$\mathrm{Log}_e\ W = -7.4302 + 3.007\ \mathrm{Log}_e\ L$ (n = 2,506)	♂; nonovigerous ♀	Gulf of Maine	Haynes and Wigley (1969)
$\mathrm{Log}_e\ W = -6.3008 + 2.702\ \mathrm{Log}_e\ L$ (n = 652)	ovigerous ♀	Gulf of Maine	Haynes and Wigley (1969)
$\mathrm{Log}\ W = -2.6469 + 2.610\ \mathrm{Log}\ L$ (n = 260)	not specified	British Columbia	Butler (1964)
$\mathrm{Log}\ W = -3.3176 + 3.0942\ \mathrm{Log}\ L$	♂ ⚥	Japan Sea	Ito (1976)
$\mathrm{Log}\ W = -2.4628 + 2.5028\ \mathrm{Log}\ L$	♀	Japan Sea	Ito (1976)
$\mathrm{Log}\ W = -3.3665 + 3.110\ \mathrm{Log}\ L$	♀ ♂ ⚥	Gulf of Maine	Rinaldo (1973)
$\mathrm{Log}\ W = -3.2506 + 3.055\ \mathrm{Log}\ L$	♀ ♂ ⚥	Gulf of Maine	Schick et al. (1981)

[1] ♀ females, ♂ males, ⚥ transitional.

Table 22.—Conversion factors and regression equations relating carapace length to total length of *Pandalus borealis*. Y = total length, X = carapace length; all measurements in mm.

Conversion factor	Carapace length/ total length	Area	Reference
5.93	$Y = 1.32 + 5.84X$	British Columbia	Butler (1964)[1]
5.76	$Y = 6.05 + 5.43X$		
5.64	—	Gulf of Maine	Haynes and Wigley (1969)[1]
5.30	—	Norway	Rasmussen (1953)[1]
—	$Y = 5.79 + 3.85X$	Japan Sea	Ito (1976)
	$Y = 17.09 + 3.45X$		
4.53	—	Gulf of Alaska	Ivanov (1963)[2]
4.6-4.7	—	Greenland	Horsted and Smidt (1956)[2]
5.05	—	Northumberland, U.K.	Allen (1959)[2]
4.95	—	Gulf of Maine	Apollonio and Dunton (1969)[2]

[1] Measured as oblique carapace length.

[2] Measured as extreme posterior lateral edge of carapace.

(1937) reported values for VO_2 of muscle tissue of 42 μL/g wet weight per h at 6°C and 69 μL/g wet weight per h at 10°C. Abercrombie and Johnson (1941) studied scaphognathite beat under different temperature exposures. Their study indicated that the right and left scaphognathites do not beat synchronously nor always at the same rate; at slow rates the beat is usually irregular with frequent motionless pauses lasting for several seconds whereas at faster rates the beat becomes fairly regular. It was also noted that the beat is highly variable between animals under similar conditions. They further showed that animal size did not affect scaphognathite beat. The beat was affected by the previous thermal history of the animal as well as the experimental conditions. The rate of beat increased with increased activity and temperature and showed a diurnal rhythm with increased rates during night hours.

Johnson (1936) also monitored movements of the scaphognathite, but under conditions of low oxygen and high carbon dioxide concentrations. Johnson found that at an oxygen tension of 3.4 cm^3/L the beat was 94/min whereas a decrease in oxygen tension to 0.95 cm^3/L resulted in an increased beat of 200/min. Conversely, as the pH was decreased from 8.3 to 6.9 the beat increased from 59/min to 185/min, i.e., scaphognathite beat is increased by low oxygen concentrations and by increased carbon dioxide. A pH of 6.6 proved fatal to the shrimp. Similar results were reported by van Heerdt and Krijgsman (1939) who showed that low pO_2 and high pCO_2 increased scaphognathite beating and high pO_2 caused a decreased rate. Wolvekamp and Waterman (1960) reported a variation of 21-145 beats/min in going from 5.5° to 16.5°C. Seiring and Hopkins (in press) found the rate of oxygen consumption of *P. borealis* to vary with the 0.85 power of body weight.

Phosphorus metabolism in the ovaries and hepatopancreas of *P. borealis* was studied by Carstam (1953), but the results were inconclusive. There was no evidence for an early alteration of phosphorus metabolism of the ovaries after removal of the eyestalks; however, it was shown that eyestalk removal may have a general effect on the phosphorus metabolism in *P. borealis* as evidenced by the changes in the phosphorus level found in the hepatopancreas of eyestalkless shrimp. It was further shown that the uptake of radioactive phosphorus into the hepatopancreas differed significantly from that in the ovary.

Carstam showed that following eyestalk removal, the amount of phosphorus in the various fractions isolated from the ovaries remained unchanged and that the amount of residual phosphorus in the hepatopancreas decreased. He showed a high turnover of the lipid soluble and residual phosphorus fractions of lipids isolated from the hepatopancreas of normal and eyestalkless animals; the turnover of residual phosphorus was found to be higher than that of inorganic phosphorus as early as 50 min after the administration of labelled phosphorus.

The following is a simplified account of hormones in the crustaceans from Barnes (1980). The hormones are either neurosecretions or are secretions of one of three endocrine tissues: the Y-organ, the androgenic gland (vas deferens), or the ovary. The center for hormone release is the sinus gland located between the two basal optic ganglia and is composed of the swollen endings of nerve fibers that originate in neurosecretory cell bodies located within the eyestalk ganglia. The cell body clusters are known as X-organs. In general, there is a hormonal interrelationship between the ovary and the X-organ-sinus gland complex, the sinus gland producing a hormone that inhibits the development of eggs during the nonbreeding periods of the year. During the breeding season, a gonad-stimulating hormone is secreted (probably by the central nervous system), egg development begins, and the ovary secretes a hormone which initiates structural changes for egg brooding such as the development of ovigerous setae on the pleopods. The development of the testes and male sexual characteristics is controlled by hormones produced by the androgenic gland which is located at the end of the vas deferens. The processes are summarized by Carpenter (1978) (Fig. 40).

These endocrine tissues in *P. borealis* have received considerable attention in an elegant series of papers by Carlisle (1959a, b, c). In his first paper (1959a), Carlisle described in detail the

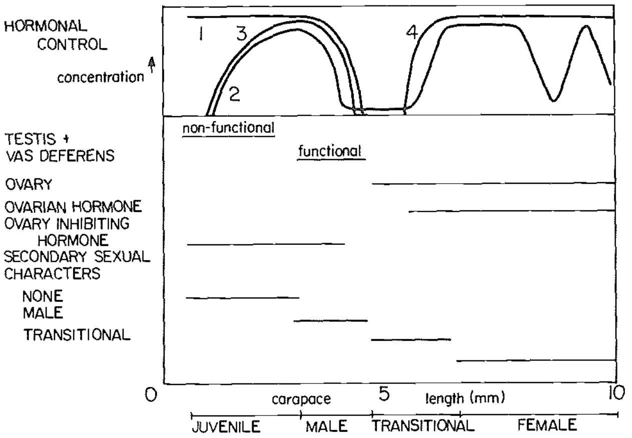

Figure 40.—A model of the physiological processes involved in protandry on the Decapoda. 1 - ovary inhibiting hormone, 2 - growth stimulating hormone, 3 - androgenic hormone, 4 - ovarian hormones (from Carpenter 1978).

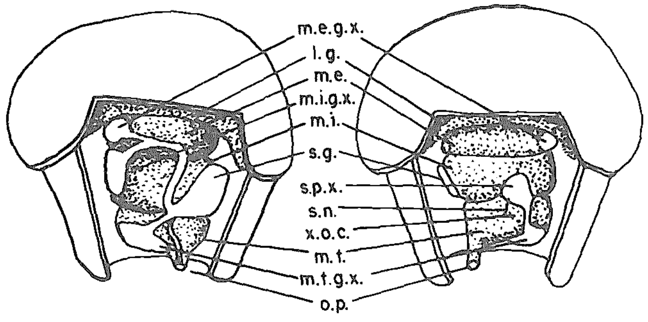

Figure 41.—Dorsal (left) and ventral (right) dissections of a left eyestalk of *Pandalus borealis*, with all the non-nervous tissue omitted. Lettering guide: l.g., lamina ganglionaris; m.e., medulla externa; m.e.g.x., medulla externa ganglionic X organ; m.i., medulla interna; m.i.g.x., medulla interna ganglionic X organ; m.t., medulla terminalis; m.t.g.x., medulla terminalis ganglionic X organ; o.p. optic lobe peduncle; s.g., sinus gland; s.n. sensory nerve of sensory port; s.p.x., sensory papilla X organ; x.o.c., X organ connective (after Carlisle 1959a).

X-organ-sinus gland complex and the vas deferens gland system of *P. borealis* (see Figs. 13, 41). He concluded that the X-organ-sinus gland complex is primitive and differs from that in other shrimp in that the sensory pore is retained and further noted that these organs are organs of internal secretion.

In two later papers (Carlisle 1959b, c), he described the function of the X-organ-sinus gland complex and the vas deferens gland system in controlling the sexual biology of *P. borealis*. In a series of experiments he demonstrated that vasectomy caused sterility, loss of libido, and degeneration of the male genital system and further that it promoted the assumption of the nonsexual condition at the next molt. It was shown that no tissue within the eyestalk had any effect upon testicular development and neither eyestalk removal nor injection of eyestalk extracts had any effect on the number of shrimp molting to the nonsexual state. Based on his experiments he concluded that the hormones of the eyestalk have little or nothing to do with the loss of the male characters at the termination of the male phase; however, it seems probable that this event is in large measure directly controlled by the secretions of the vas deferens gland. Other endocrine organs implicated in the control of the male phase are the follicle cells of the testis (Allen 1959) and the endocrine complex of the protocerebrum (Carlisle and Jenkin 1959). Carlisle (1959b) concluded that the immediate cause of the termination of the male phase is the degeneration of the vas deferens gland. Cessation of spermatogenesis after eyestalk removal was later reported by Charniaux-Cotton (1967).

In the final paper of the series, Carlisle (1959c) showed that ovarian growth and maturation is regulated at least in part by the X-organ-sinus gland complex and that no other tissue within the eyestalk had any action upon ovarian growth. He also found that the change from the nonsexual condition to the functional female state was inhibited by a hormone from the same source and concluded that since the two inhibitions showed such a high degree of correlation they probably represent two responses to the same hormone.

Color change in crustaceans is controlled by hormones produced by neurosecretory cells and stored in the sinus gland of the eyestalk. Due to its relatively large size (fresh weight of single live eyestalk is 15-20 mg; Ostlund and Fange 1956), *P. borealis* has been a favorite experimental animal for use in hormone extraction studies. Edman et al. (1958) isolated a red-pigment-concentrating substance from the eyestalk of *P. borealis*. They characterized the substance as being of very high biological activity, inactivated by chymotrypsin, trypsin, and by prolonged treatment with strong HCl. They noted that the substance had acidic properties and proposed it to be a polypeptide. In later studies (Josefsson and Kleinholz 1964; Kleinholz and Kimball 1965; Josefsson 1967), a method for isolation and purification of the eyestalk hormones was developed, followed by separation and purification of distal retinal pigment hormone (DRPH) and red-pigment-concentrating (RPH) hormone, erythrophore-concentrating hormone (ECH), and melanophore-dispersing hormone (MDH). Fernlund and Josefsson (1968a) isolated both the RPH and the DRPH and confirmed that the RPH is a peptide and showed that it contains eight amino acids (aspartic acid, glutamic acid, glycine, leucine, phenyalanine, proline, serine, and tryptophan). They estimated a minimum molecular weight for the hormone of 1,000. Fernlund (1968) and Fernlund and Josefsson (1968b) later used these purified hormones in bioassay studies of *Palaemon adspersus*.

Hjort (1922) first determined the presence of vitamin A activity in *P. borealis*. Lambertsen and Braekkan (1955) reported the occurrence of a new vitamin A_1 isomer in the eyes of *P. borealis* and postulated that it was the Δ-3,5-di-cis-isomer previously postulated by Hubbard and Wald (1952). Barnholdt and Hjarde (1957) studied the isomers of this vitamin and presented the following summary:

"In fractional chromatography of the unsaponifiable fraction from the eyes of deep-water prawns the vitamin A_1 present was found to separate into five components: *a*, *b*, *c*, *d*, and *e*. In two instances the relative proportions of the different isomers present, expressed by $E_{325\ m\mu}$ measured on the collected fractions were found by chromatography to be as follows:

1. a:b:c:e = 0.8:52:9:38 (*d* was incompletely separated from *c* and *e*, the quantity of *d* may be estimated to be about 0.5-1%).
2. a:b:c:d:e = 1.5:49:17:1.5:31.

"The substances obtained were subjected to a number of identification tests: isomerization with iodine as catalyst, formation of anhydro vitamin by means of hydrogen chloride, determination of $E_{620m\mu,\ Carr\text{-}Price}/E_{m\cdot v\cdot max}$ and the maleic anhydride reaction. The spectrophotometric properties of the substances have also been examined for the purpose of establishing their identity.

"The results obtained suggest that substances *a*, *b*, *c*, and *e* are identical with 11,13-di-*cis*, 11-mono-*cis*, 13-mono-*cis* and all-

trans vitamin A_1, respectively, while the small quantities of substance *d* available have rendered the identification of this substance less certain. The possibility that substance *d* is 9,13-di-*cis* vitamin A_1 is discussed. In a preparation marketed by Messrs. Hoffmann-La Roche & Co., Basle, under the name of 'Vitamin A, Feed Grade', the presence has been ascertained of an isomer the properties of which agree with those of substance *a* and 11,13-di-*cis* vitamin A_1."

In other studies on vitamin content of *P. borealis*, Lunde (1938) reported 60 IU/g of vitamin D in whole raw shrimp and Lunde et al. (1938) gave a concentration of 0.27 μg/g for thiamine. They also reported riboflavin levels of 1.6 μg/g and 7.7 μg/g for body and eggs, respectively.

Only one study has been carried out concerning the pigments of *P. borealis*. Tsukuda (1963) separated the pigments into three fractions: astaxanthin, astacene, and a substance he considered to be carotene. Most of the pigment was esterified astaxanthin; the amount of astacene formed from astaxanthin after death was scarce and the concentration of carotenelike pigment was low. Concentration of astaxanthin was measured using the value $E1\%_{1cm}$ (478^{mu}) = 2.200 for pure astaxanthin in acetone. He reported more than 90% of the pigment contained in the exoskeletons with a wide variation between individuals (6.6-16.0 mg%). Astaxanthin was scarce in the muscle tissue, occurring only in the epidermis.

Svedberg and Pedersen (1940) reported a sedimentation rate of 17.4×10^{-13} cm/s per dyne at 20°C for *P. borealis* haemacyanin and Gardiner (1972) reported a molecular weight of 397,000; however no reference was given.

3.45 Molting

As in other crustaceans, copulation is associated with a nuptial molt in *P. borealis* and egg extrusion follows with a few days. In addition, both molting and ovarian development are controlled through the eyestalk hormonal complex.

Stickney and Perkins (unpubl. data) have shown that molting is also influenced by temperature. Shortly after the time of egg hatching, shrimp undergo a molt. Their molting records (Fig. 42) indicate 2-4 additional molts including the nuptial depending on temperature. At 4° and 6°C, a few shrimp appeared to have laid their eggs following the second of these additional molts. This second molt occurs earlier at 6° that it does at 4°, and the first egg laying comes earlier at 6° than at 4°. The second additional molt comes earlier yet at 8°C, in fact, too early for the ovaries to be mature enough for ovulation. Egg laying must therefore wait until at least the third molt to begin. This event occurs later than the second molt at 6°, hence egg laying at 8° is later than at 6°.

3.45 Size and Age

Size in *P. borealis* is directly related to age which is, in turn, related to geographic region. Direct determination of age is not possible and two common indirect methods have thus been employed: length-frequency distributions and examination of sex-related characteristics. The accepted measurement for use in length-frequency determinations is the oblique carapace length (OCL) (Fig. 9) measured from the posterior margin of the orbit to the posteriodorsal margin of the carapace.

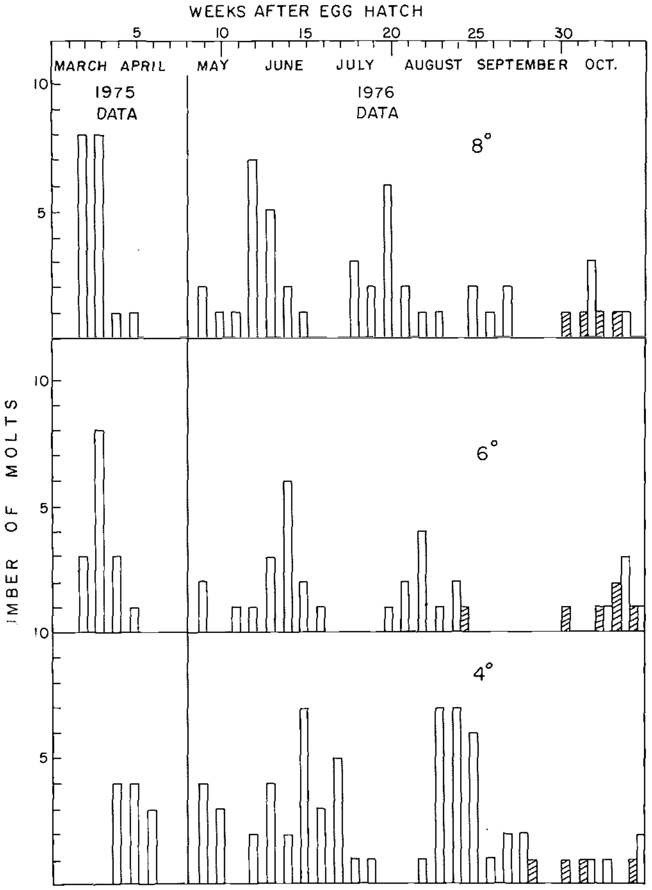

Figure 42.—Molting frequency at three temperatures of *Pandalus borealis* during the period of ovogenesis. Unshaded bars represent the weekly total of individual molts; shaded bars represent the weekly total of females which extruded their eggs (from Stickney and Perkins 1977).

As a result of a NAFO (Northwest Atlantic Fisheries Organization) workshop on shrimp ageing held in 1981, the following guidelines for ageing *P. borealis* were recommended for consideration in sampling, analysis of data, and estimation of age (Frechette and Parsons 1983). Each sample should contain a minimum of 500 individuals. The carapace length should be measured to the nearest 0.1 mm with subsequent groupings to 0.3 mm or 0.5 mm intervals. Methods of collecting and combining samples should be standardized. Randomization of commercial sampling, stratification of age groups by depth, selectivity and availability problems with small shrimp, diel vertical variablity in distribution, weighting of sample length frequencies, and size composition of discards should all be considered. Computer analysis of length-frequency distributions was found superior to graphical methods, but should be accompanied by sex and reproductive stage identification.

The workshop also identified and explored in detail the following problem areas: growth in shrimp is discontinuous; mortality is poorly understood with a wide range in natural mortality estimates (0.2-0.8); there may be fast-growing and slow-growing year classes in a population; the frequency of molting is unknown; the growth rate in larvae is uncertain; gear selectivity for small shrimp and the availability of young shrimp to the sampling gear is unknown; spawning characteristics may be differentially interpreted; also, the degree of accumulation of year classes in the last female mode is unknown.

The NAFO workshop recommended that the above-mentioned problems, especially age determination, receive priority attention from researchers in the field.

McCrary (1971) proposed the use of the sternal spines as a means of differentiating between females which have previously spawned and those that have not. Figure 43 shows the sternal spines at various stages of development. The development of these spines can be a useful tool during periods between successive spawning seasons for determining the number of females which survive one or more spawnings.

Maximum attained size in *P. borealis* appears to be approximately 37 mm CL or 182 mm (Ito 1976) total length (see Table 3).

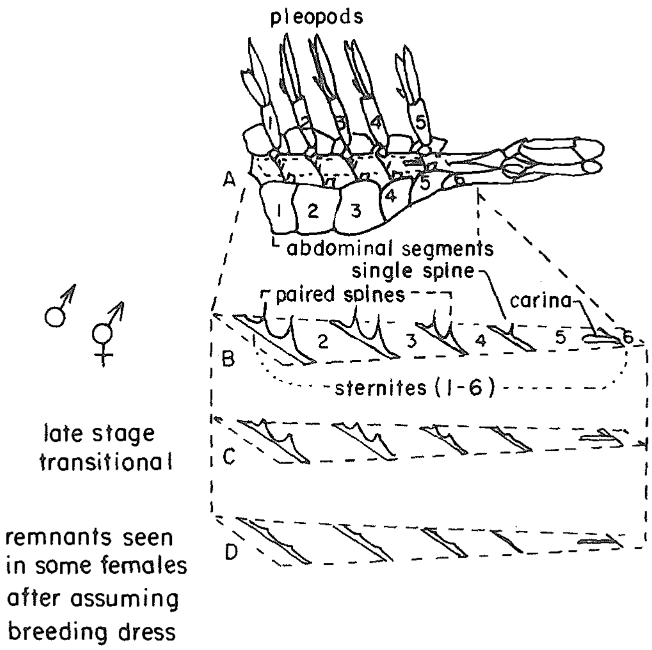

Figure 43.—Diagrammatic ventral view of the abdomen of a pandalid shrimp showing sternal spines (after McCrary 1971).

3.5 Behavior

3.51 Migrations and local movements

Larval movement is more or less at the mercy of currents during their pelagic existence. No directed activity has been ascribed to them in terms of selecting tide currents of various directions and heights off bottoms to maintain geographical position.

Juvenile migration from shallow water to the deeper shrimp beds has been documented by Berkeley (1930) off British Columbia, Hjort and Ruud (1938) off Norway, Horsted and Smidt (1956) off west Greenland, Apollonio and Dunton (1969) in the Gulf of Maine, but was not found near the Pribilof Islands in the Bering Sea by Ivanov (1967b).

Adult migration has been documented by many authors and is reviewed in sections 2.22 and 2.3 as to extent, direction, mode, and time of season of the movements. Some effects of the migrations and some anomalies are worth mentioning here. Dow (1981) indicated that during a period of extreme temperature (high) stress in the Gulf of Maine during the mid-1950's, the normal shoreward migration of berried females did not occur. In the same area, Haynes and Wigley (1969) showed incomplete shoreward migration of berried females during a period of great abundance and lower temperatures.

In searching for a mechanism that explained migration, Apollonio and Dunton (1969) hypothesized that berried females migrated shoreward in the early winter seeking colder water. Similarly the offshore migration of the immature males was driven by a quest for lower temperatures offshore in the spring/early summer.

Smidt (1965) and Carlsson and Smidt (1978) found that fluctuations in stock density in fjords in west Greenland are closely correlated with an increase in bottom water temperature caused by inflow of warm bottom water. The migration of adult *P. borealis* into these fjords was proved by recaptures from tagging experiments carried out by Horsted (1969).

Carlsson (1979) posed a relation between vertical migration and horizontal movements based on general drift of shrimp off west Greenland and known current structure. Hoydal (1978b) indicated that vertical migration influenced distribution and affected catch per unit effort measurements which caused assessments based on bottom trawls to underestimate stock size.

Ivanov (1967b) has shown seasonal migrations of adult *P. borealis* of 30-40 km near the Pribilof Islands in the Bering Sea in response to annual shifts in the boundary between the cold upper zone and the warm bottom zone.

3.52 Schooling

Pandalus borealis is a schooling species that aggregates in relatively dense patches. The patches are often segregated by size (see section 2.22). During migration in the Gulf of Maine, the females remain aggregated as they move inshore and become more densely packed on the inshore beds. This migration causes segregation of the year classes for much of each year. Vertical migration also causes some segregation of year classes especially because berried females remain on bottom. Barr (1970a) reported that smaller shrimp migrate further vertically in Alaska.

Shrimp species can be mixed in the catches (see section 4.6) but Ivanov (1967b) and Squires (1970) have found that in schools of great density, *P. borealis* occurs almost to the exclusion of all other species.

3.53 Responses to stimuli

The effects of temperature shock on adult *P. borealis* were described by Abercrombie and Johnson (1941). They reported that upon transfer from low to high temperatures the shrimp exhibited a violent activity followed by a period of "depression," i.e., the animals lay flat on the ventral surface of the thorax with their legs appearing too weak to support them (at 11°C); at 11°C this soon disappears but the response lasts some time at 14°C. On going from 5° to 15°C, no spasm of activity was noted and the animals fell on their sides and recovered after a few hours. At 18°-20°C the shrimp fell on their sides, usually with their tails curled up, twitching slightly, the scaphognathites working very irregularly. Seldom did any shrimp recover from this prostration.

On going from high to low temperatures there was some activity accompanied by a complete loss of equilibrium. The animals swam or lay on their backs or sides; recovery was gradual and lasted about an hour with no period of depression.

Thermal death was shown to be a slow process. Abercrombie and Johnson (1941) demonstrated that the period of depression may last hours or days (at lower lethal temperatures) and eventually the animals fell to their sides but continued to live for many hours. Finally, the scaphognathites slowed and stopped at which point the animals failed to respond to any stimulus. The shrimp are transparent at death below 17°C whereas just before death at higher temperatures many animals became opaque, especially in the abdominal region, with the tail flexed under the carapace. It was further shown that survival times could be increased by gradual acclimation to higher temperatures (see Fig. 44).

Stickney and Perkins (unpubl. data) studied temperature preference in adult *P. borealis* by exposing the shrimp to a temperature gradient system. Although none of the individuals exhibited a strong response to temperature change, the general trend was toward cold water and they suggested that egg-bearing shrimp may gravitate towards the coldest water available to them as they encounter gradients (Table 23).

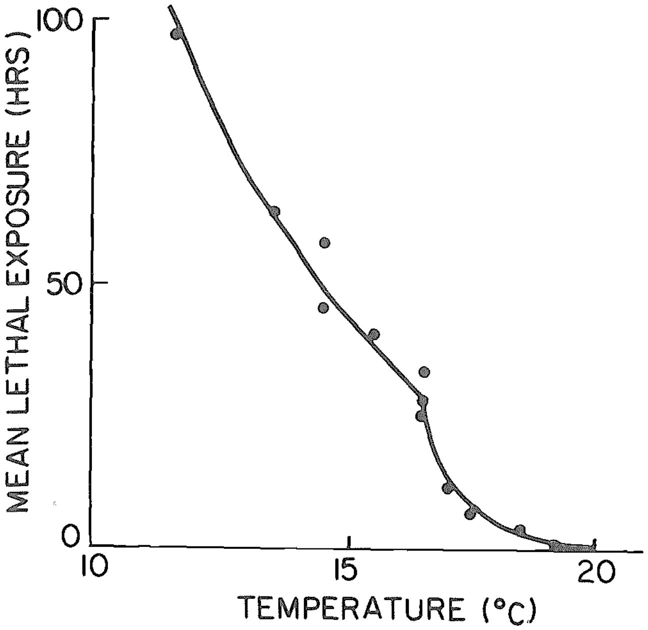

Figure 44.—Mean lethal temperatures for *Pandalus borealis* (from Abercrombie and Johnson 1941).

Table 23.—Responses of ovigerous shrimp with three levels of temperature adaptation to temperature gradients. Scores of < 42 indicate direction of response toward cooler water; > 42 toward warmer water (after Stickney and Perkins 1977).

Gradient range and direction	Adaptation temperature		
	4°	6°	8°
4°-6°C	36.75	35.08	39.16
6°-4°C	50.30	39.40	43.83
Corr. for bias	43.52	37.25	41.49
6°-8°C	44.17	35.47	35.17
8°-6°C	46.83	28.08	38.91
Corr. for bias	45.50	31.78	37.04
8°-10°C	38.42	39.90	32.58
10°-8°C	50.08	36.40	45.08
Corr. for bias	44.25	38.15	38.83

4 POPULATION

4.1 Structure

4.11 Sex ratio

Pandalus borealis is a protandric hermaphrodite and as such the sex ratio at any one time in the population is a function of natural mortality, fishing mortality, and recruitment. Since migration occurs in certain populations, the perceived sex ratio is also a function of location and season of sampling.

The sex, size, and age ratios of protandric hermaphrodites are inextricably interwoven. The sex and size at increasing ages during the spawning season are shown at spawning season for 10 different populations of *P. borealis* in Table 3.

The sex, age, and size ratio of the catch of *P. borealis* is dependent on the selectivity of the gear used, the time of year, and location of effort. In the Gulf of Maine, the winter fishery inshore is directed primarily at the females that have migrated inshore to release their larvae. Later in the spring as the fishery follows the shrimp back offshore, the mean size of shrimp caught drops as the gear encounters the males and transitionals in the offshore beds.

The sex ratio on the spawning grounds is dependent on the relative strengths of the year classes since the males from one year class are mating with females from a previous year class. Some populations have some degree of early maturing females, either primary or secondary, which will influence the sex ratio.

4.12 Age composition

There is no method for mechanically determining age in *P. borealis* since all hard parts are shed with each molt. Thus age determination has been accomplished by separation of size groups from length frequency distribution or by following an unusually large year class through time (Skuladottir 1981a). Methods of determining age were reviewed by Frechette and Parsons (1983) (see section 3.46).

The age composition of a population of *P. borealis* is affected by the same determinants as sex ratio (see section 4.11). Age distribution of the catch, age at first capture, and density of age groups are all affected by selectivity of the fishing gear and intensity of fishing (see sections 5.41 and 5.42). Age at maturity for males ranges from 1.5 yr to 3.5 yr and for females ranges from 1.5 yr to 5.5 yr (Table 3). Rasmussen (1953) found that maturity is delayed by colder conditions. Skuladottir et al. (1978) have demonstrated as much as 2 yr difference in age at first maturity for females between populations in different Icelandic fjords. Maximum age is also greater towards the Arctic with Iceland and Spitsbergen showing 11+ and 8+ yr, respectively. In most of the areas studied, *P. borealis* lives for 4+ to 5+ yr (Table 3).

4.13 Size composition

The size composition of a population is more readily determined from research surveys than from commercial catches due to the smaller meshed nets employed on the surveys, but catches are still biased towards the larger shrimp. Length frequencies of *P. borealis* from research surveys are common throughout the literature but selected examples by area are: Allen (1959) for Northumberland; Apollonio and Dunton (1969) for the Gulf of Maine; Butler (1964) for British Columbia; Frechette and Dubois (1974) for the Gulf of St. Lawrence; Horsted and Smidt (1956) for west Greenland; Ivanov (1964a) for the Bering Sea; Jackson (1980) for the Gulf of Alaska; Jensen (1967) for the Skagerrak; Rasmussen (1953) for Norway; Sigurdsson and Hallgrimsson (1965) for Iceland; and Squires (1970) for Labrador and Newfoundland.

The length frequency distribution of the commercially caught shrimp has been reported by Rasmussen (1967b) in Norway, by Jensen (1967) in the Skagerrak and on Fladen in the North Sea, by Howard (1977a) in Northumberland, by Ulltang and Oynes (1978a, b) in west Greenland, by Parsons et al. (1981) in Labrador and Newfoundland, by Frechette and Parsons (1981) in the Gulf of St. Lawrence, and by Clark (1981), Diodati (1980),[7] Rinaldo (1976), and Schick (1983) in the Gulf of Maine. A marked decrease in the size composition of the commercial catch was noted by Jensen (1967) during the development of the fishery in the Skagerrak.

The size composition of many populations varies with depth, distance from shore, time of day, and season. Distributional differences have been described in sections 2.2 and 2.3.

The size at which shrimp are first captured in the various commercial fisheries has little meaning since in all cases very few of these smaller individuals are taken. Table 24 lists size at first capture and approximate mean size of the first size class taken in six separate fisheries.

The size at maturity for males and females is reviewed for 10 populations in Table 3. Rasmussen (1953) noted a constant size at maturity off Norway whereas age at maturity of the individuals might vary. .Skuladottir et al. (1978) has documented a range of sizes at maturity between Icelandic fjords and over time in the same fjord as a population was depleted through fishing.

The maximum size measured for *P. borealis* varies from one area to another (Table 3). The maximum recorded dorsal carapace length is 37 mm (Ito 1976) and the maximum recorded total body length is 182 mm (Haynes and Wigley 1969).

Density of size groups can be estimated from catch per unit of effort by age, but has not been specifically calculated in the literature.

The length-weight relationship for ovigerous females and for non-ovigerous shrimp from several populations is reviewed in Table 21. Schick et al. (1981) has shown differences in the length-weight relationship over time in the same area and between areas at the same time in the Gulf of Maine.

Table 24.—Size at first capture and mean size of the first size mode taken in six fisheries of *Pandalus borealis*.

First size mode: mean dorsal carapace length[1] (mm)	Location	Size at first capture (DCL mm)	Reference
18-20	Labrador	15	Parsons et al. (1981)
12-17	Fladen	10	Howard (1977b)
21	W. Greenland	11	Ulltang and Øynes (1978a)
15	St. Lawrence	11	Frechette and Parsons (1981)
18	Gulf of Maine (winter)	15	Schick (1981)
14	Gulf of Maine (spring)	10	Clark (1981)

[1] Approximate.

4.2 Abundance and density

4.21 Average abundance

Estimates of the size of populations are biased by the limitations of the selectivity of the gear used to sample the populations. The most common method of sampling utilizes otter trawl with a fine mesh liner in the cod end. Using commercial catches to estimate population size is limited by the relatively large mesh size. Another method involves the use of bottom photography (Kanneworff 1978a, b, 1979, 1981). Taking a series of photographs which represent a known area of the ocean bottom and counting the number of shrimp per area will give average density. Multiplying this average value by the total bottom area introduces another source of error in that the extent of bottom area characterized by the photographs is difficult to determine.

Estimates of fishable biomass have been made for many of the *P. borealis* fisheries of the world. These estimates are usually based on a randomized survey of the area in question which may be stratified by depth for greater accuracy of the estimate. ICES (1977) periodically assesses stocks of *P. borealis* off Norway, in the North Sea, in the Skagerrak, and off Iceland. NAFO (1981) periodically assesses stocks of *P. borealis* off Greenland (Hoydal 1978a, b and others, see NAFO assessment meeting series). Canada assesses the shrimp stock off Labrador (Parsons et al. 1981), off Baffin Island (Jones and Parsons 1978), and in the Gulf of St. Lawrence (Frechette and Parsons 1981). Many other papers on shrimp assessment in these areas have been presented at NAFO meetings. The United States assesses the stock size of *P. borealis* in the Gulf of Maine (Anthony and Clark 1980; Rinaldo 1976; NSSC 1976, 1978, 1979a, 1980; NSTC 1981, 1982, 1983) and in the Gulf of Alaska (Gaffney 1977a, b, 1978; Jackson 1980).

4.22 Changes in abundance

Changes in abundance caused by hydrographic conditions have been documented in several areas. Off west Greenland *Pandalus borealis* will move from area to area depending on bottom water temperature and can even suffer mass mortality if the bottom water gets too cold (Horsted and Smidt 1956). Abundance is controlled by hydrographic conditions in the Bering Sea where circular gyres hold larvae in areas that enhance survival. *Pandalus borealis* survives well along bottom and mid-water interfaces in the Bering Sea (Ivanov 1967b). At the southern limit of the range of *P. borealis* in the Atlantic, wide fluctuations in abundance have been correlated with shifts in average annual temperature by Anthony and Clark (1980) and by Dow (1963, 1964, 1966, 1967a, b, 1973, 1977a, b, 1979).

Changes in abundance of *P. borealis* caused by competition for food have not been identified. Changes in abundance caused by predation have been documented by showing changes in relative abundance of predators and shrimp in several areas. Bowering and Parsons (1981) have documented an increase in the abundance of the Greenland halibut in two Labrador channels and are assessing the effect of the increase of this predator on the shrimp population in the area.

Changes in abundance have been correlated with heavy fishing pressure in several areas. Some of the populations have recovered and some have not. Populations at the specie's northern limit tend to reproduce slowly and less successfully and these have been the ones that have not recovered. Ivanov (1967b, 1974) documented the development of an intense shrimp fishery in the Pribilof Island area and the subsequent population decline.

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[7] Diodati, P. J. 1980. Preliminary report: Monitoring of the northern shrimp fishery during the 1980 open season, February 15-May 31, 1980. Unpubl. manuscr., 17 p. Cat Cove Marine Laboratory, Massachusetts Division of Marine Fisheries, 92 Fort Ave., Salem, MA 01970.

4.23 Average density

Annual mean density

Annual mean density can be obtained from photographic bottom surveys or from catch per unit of effort data from either research surveys or commercial sampling. Where trawl gear is used, the estimate of the number of shrimp is biased by the selectivity of the gear with the research gear having generally finer meshed nets than in the commercial gear. Annual sampling of the population gives at least relative numbers that are comparable with each other for assessing trends in abundance or density.

Density of adult females

Commercial fisheries throughout the world tend to concentrate effort on the females due to their larger size. Thus commercial sampling will give a better estimate of density of females than of the population as a whole.

4.24 Changes in density

Landings per unit of fishing effort

Catch per unit of effort (CPUE) is a measure of density of the population. CPUE data have been reported for several *Pandalus borealis* fisheries (Bennett 1977; Butler 1969; CAFSAC 1981,[8] 1982;[9] Carlsson et al. 1978; Clark 1982; Clark and Anthony 1981; Cormier 1981, 1982; Dupouy et al. 1981a, b; Frechette and LaBonte 1981; Hoydal 1978b; ICES 1977, 1979; ICNAF 1979a, b; NAFO 1981; NSSC 1976, 1978, 1979a, b, 1980; NSTC 1981; Parsons et al. 1981, 1983; Rinaldo 1973, 1976, 1981; Schick 1983; Schick et al. 1981; Schick and Sampson 1983; Skuladottir 1981b; Smidt 1965; Ulltang and Oynes 1978b).

Variations with depth

Pandalus borealis is found within a depth range of 9 to 1,450 m. Some populations show seasonal migration where depth (average) of the population (or of certain year classes of the population) changes. In the Gulf of Maine, females migrate inshore in the winter where they may be found in depths as shallow as 45 m. Along the Maine coast the fishery is perpetrated at an average depth range of 45 to 110 m. In the Massachusetts fishery, the winter fishery is similar to Maine's, but the spring fishery follows the shrimp into deeper water (150-185 m).

Seasonal variations in available stock

The winter fishery for *P. borealis* in the Gulf of Maine is directed at the ovigerous females after they migrate inshore to release their larvae. While inshore, the females are concentrated on smaller beds, which makes them more available. If the females have not arrived inshore by the time the fishing season starts, the majority of the fishermen along the Maine coast will, in general, wait for them to arrive inshore rather than go offshore in search.

4.3 Natality and recruitment

4.31 Reproduction rates

The egg production rate or fecundity of *Pandalus borealis* females has been measured for many of the populations (see section 3.17). In all cases the fecundity of the individual females was found to increase with size and ranged from 600 to about 4,900 eggs. The survival of the eggs to the time of larval release shows some attrition based on egg counts versus size of female throughout the berried season. In the Gulf of Maine, part of this attrition is due to a peridinian parasite that was noticed by Haynes and Wigley (1969) and Apollonio and Dunton (1969) as "white" or "non-viable" eggs and was identified by Stickney (1978) (see section 3.21).

Larval survival is low, but relative survival from year to year has been monitored by Stickney and Perkins (unpubl. data) in the Gulf of Maine. Forecasting future abundance from larval survival has proved difficult.

4.32 Factors affecting reproduction

The effect on larval survival of density-dependent factors such as cannibalism, food supply, and predation, is discussed in section 3.22. The fecundity of females in the Gulf of Maine has been shown to be inversely related to abundance (Stickney and Walton footnote 3) and offshore bottom temperature (Apollonio et al. 1984). Whether this represents an inverse correlation between abundance and temperature or whether this is a density-dependent effect caused possibly by competition for food is unknown.

A fishery directed at the berried females, such as is the case in the Gulf of Maine, certainly affects the reproductive capacity of the population. The degree of effect is couched in a parent-progeny relationship which is unknown. Management efforts in Iceland, Alaska, and British Columbia are geared towards protecting the berried females (see Table 31).

Occasionally physical effects on reproduction are documented. Horsted and Smidt (1956) noted that a mass mortality of adults occurred in a west Greenland fjord during an exceptionally cold winter and that it was 4 to 5 yr before the shrimp population recovered in the fjord. Another physical factor, unfavorably high temperature at the southern extremes of the range of *P. borealis*, has been documented as being related to extreme fluctuations in abundance with reproduction stated as being the most sensitive and therefore the most likely affected biological function of the population (Dow 1963, 1964, 1966, 1967a, 1973, 1977a, b, 1979, 1981; Apollonio and Dunton 1969).

4.33 Recruitment

Recruitment to the fishable stock refers to the numbers or weight (biomass) of younger shrimp that are entering the fishery. Recruitment is measured by analysis of length-frequency distributions for relative or actual year class strength, by photographic surveys of the bottom, by analysis of length-frequency distributions and CPUE by age class in the commercial catch, and by analysis of discards of small shrimp in the commercial catch. Recruitment is one of the best indicators of the condition of the stock. Recruitment varies widely from year to year in several

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[8] CAFSAC. 1981. Advice on some invertebrate stocks: 1. Shrimp stocks in Divisions 2HJ. 2. Shrimp stocks in Divisions 2G and 3K. 3. Shrimp stocks in Ungava Bay and Eastern Hudson Strait. Can. Atl. Fish. Sci. Advis. Comm., Advis. Doc. 81/3, 9 p. CAFSAC Secretariat, Department of Oceans and Fisheries, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

[9] CAFSAC. 1982. Advice on the management of shrimp stocks in the Gulf of St. Lawrence in 1982. Can. Atl. Fish. Sci. Advis. Comm., Advis. Doc. 82/7, 4 p. CAFSAC Secretariat, Department of Oceans and Fisheries, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

populations for unknown or poorly understood reasons. Population models for *P. borealis* have not been successful in long range predictions of population size because they have not been able to adequately define the recruitment process. Thus catch recommendations have been limited to assessments based on CPUE trends, length frequencies, and biomass estimates. Rinaldo (1976) calculated recruitment as the difference between the estimated stock size and the survivors from the previous year in his assessments of the Gulf of Maine stock.

4.4 Mortality and morbidity

4.41 Mortality rates

Mortality is assumed to be high in *Pandalus borealis*, especially in the females after spawning. Frechette (1981) gave a mean total mortality of 1.0 with a range of 0.6 to 1.4 for populations of *P. borealis* in the Gulf of St. Lawrence based on annual biomass estimates and size distribution. The instantaneous total mortality (Z) as defined by Gulland (1969)

$$Z = -\log_e \frac{N_1}{N_0}$$

where N_1 = abundance of a cohort at the end of a given time interval, and
N_0 = abundance of a cohort at the beginning of a given time interval

was used by Anderson (1978)[10] to show the mortality coefficient (Z = 0.65) between year classes 3 and 4 and year classes 5 and 6 from successive trawl surveys in the Gulf of Alaska. Anderson (1981) followed a specific year class (1971) for 7 yr and calculated Z annually between 1974 and 1978 (Table 25). Anthony and Clark (1980) calculated Z for the Gulf of Maine population from 1968 to 1976 from NMFS catch data utilizing a catch curve analysis and obtained instantaneous fishing mortality (*F*) by subtracting instantaneous natural mortality (*M*) (*M* = 0.25, Rinaldo 1976) from Z. Rinaldo (1973, 1976) utilized the program NORMSEP based on an algorithm developed by Hasselblad (1966) to separate four size modes (assumed year classes) from the length-frequency distributions of *P. borealis* in the annual state of Maine shrimp survey and calculated Z for each size made. Several authors have utilized this data in their assessments of the Gulf of Maine population (Clark 1981, 1982; Clark and Anthony 1981; NSSC 1979a). More recent analysis indicates a possibility of only three size classes in the Maine survey data (Schick 1981). Frechette and LaBonte (1981) calculated Z for the northwest Gulf of St. Lawrence from swept area biomass estimates and size class separations of length-frequency distributions utilizing the program NORMSEP (Table 26). They calculated *F* using the same size distribution data and the total annual catch and obtained *M* by subtracting *F* from Z. LaBonte (1980) found Z ranged from 0.71 to 0.86 in the north Anticosti area of the Gulf of St. Lawrence by interpreting the parameters of the Von Bertalanffy growth equation. Frechette and Parsons (1981) calculated Z from the same region for males and females based on swept area biomass estimates and age classes determined from length-frequency distributions (Table 27). Their estimates agreed closely with LaBonte (1980).

Table 25.—Total instantaneous mortality coefficients (Z) for pairs of age groups of the 1971 year class, Pavlof Bay, standardized by survey effort.[1]

	Age (yr)			
Years	3/4	4/5	5/6	6/7
1974/1975	0.65			
1975/1976		−0.26		
1976/1977			0.66	
1977/1978				1.26

[1] Effort expressed as total miles towed.

Table 26.—Mortality rates in the northwest Gulf of St. Lawrence, 1974-76. From Frechette and LaBonte (1981).

Years	Class III$^+$IV$^+$→IV$^+$	III→IV$^+$	II→III
(a) Instantaneous Rate of Total Mortality (*Z*)			
1974-75	0.75	—	—
1975-76	1.03	0.54	0.67
(b) Instantaneous Rate of Fishing Mortality (*F*)			
1974-75	0.27	0.38	0.38
1975-76	0.23	0.31	0.28
(c) Instantaneous Rate of Natural Mortality (*M*)			
1974-75	0.48	—	—
1975-76	0.80	0.24	0.39

Table 27.—Instantaneous total mortality rates for males and females in the North Anticosti area of the Gulf of St. Lawrence 1977-80. From Frechette and Parsons (1981).

Year	Females[1] III-IV$^+$	Males II-III
1977-78	—	0.87
1978-79	0.62	0.45
1979-80	0.91	0.42

[1] Assumes that the IV+ group is an accumulation of older age groups.

Natural mortality is recognized as being of prime importance in assessing populations of *P. borealis*. No direct method of determining natural mortality is known. Recent work on predator-prey relationships involving *P. borealis* (Bowering and Parsons 1981) is a beginning attempt to quantify natural mortality. Rinaldo (1973) estimated instantaneous natural mortality as the *Y* intercept from a regression of effort (boat days) against total mortality (Z) by year class for 1968 through 1972. Rinaldo's estimate (*M* = 0.25) must be regarded as an approximation. Values of 0.3 and 0.2 were chosen by Skuladottir (1979) for assessments in Iceland. An ICES working group (ICES 1977) estimated an *M* of 0.5 for a population of *P. borealis* southwest of Iceland utilizing a "catch curve" from a deviation method analysis of size composition data. Skuladottir (1979) chose *M* = 0.3 and 0.2 in several assessments of a population of *P. borealis* in Arnarfjordur, Iceland, because

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[10] Anderson, P. J. 1978. Growth and mortality estimates for a population of pink shrimp *Pandalus borealis* from the western Gulf of Alaska. Unpubl. manuscr., 16 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Kodiak, AK 99615.

predation was assumed to be lower in this fjord than in others due to a smaller population of large cod in the fjord. ICES (1977) chose levels of $M = 0.5$ and 1.0 in yield assessments of the Fladen and Skagerrak due to faster growth and fewer year classes on these grounds than in Iceland.

The instantaneous fishing mortality coefficient, F, has been calculated from catch by age class by several authors and has also been calculated by subtracting M from Z. Anthony and Clark (1980) estimated F by calculating instantaneous total mortalities from catch by age class in the Gulf of Maine fishery and subtracting M (Rinaldo's value of 0.25) (Table 28). In another assessment, Clark and Anthony (1981) used Z from the Maine annual research survey and subtracted M (= 0.25) to obtain F. Skuladottir (1979) calculated F for a series of age classes at two levels of M from a cohort length analysis (Jones 1974) and a cohort age analysis (Pope 1972) (Table 29). Frechette and LaBonte (1981) calculated F for each class from total commercial catch and catch by age class from survey data.

Variations in mortality from year to year are to be expected with changes in predation, fishing effort, and other biological and abiotic factors.

4.42 Factors causing or affecting mortality

Several factors affect the mortality rates of *Pandalus borealis*. Predation by fish has been documented by several authors and is reviewed in section 3.34. Food supply for larvae is reviewed in section 3.22. Physical factors have been found to have profound effects on populations of *P. borealis* and are reviewed in section 2.3. The major physical factor affecting this is temperature. Horsted and Smidt (1956) documented a mass mortality in a west Greenland fjord when sea temperature fell to −1.6°C. Optimum temperature range by month was calculated by Dow (1964) from a correlation of sea surface temperature and shrimp landings in the Gulf of Maine (Table 30). Wide fluctuations in abundance in the Gulf of Maine have been correlated with temperature by Dow

Table 28.—Landings, indices of abundance, calculated abundance, recruitment, and fishing mortality (F) estimates for the Gulf of Maine northern shrimp stock. After Anthony and Clark (1980).

Year	Landings (metric tons)	Commercial catch/day fished[1] (kg)	Catch/30 min tow Maine research surveys (kg)	Abundance (thousand metric tons)	Recruitment (thousand metric tons)	Instantaneous fishing mortality[2] (F)
1958	2					
1959	7					
1960	41					
1961	31					
1962	176					
1963	254					
1964	423	962				
1965	949	1.352				
1966	1.766	1,887				
1967	3.171	2.549				
1968	6.610	1.855	56.9	15		.71
1969	12.824	2,790	31.2	27	22	.75
1970	10.647	1.556	40.8	24	14	.71
1971	11,130	2.263	9.4	14	5	1.95
1972	11.095	1,746	6.9	15	14	1.72
1973	9.405	1,787	9.0	18	15	.88
1974	7.986	1,433	4.5	10	4	1.95
1975	5.298	1.383	8.1	8	7	—
1976	1.066	857	5.4	5		.89
1977				3		
1978				1		

[1] Combined vessel classes 0-50 GRT and 51-150 GRT.

[2] Instantaneous total mortalities calculated from catch curve analyses. An assumed rate of natural mortality ($M = 0.25$) was subtracted to estimate F.

Table 29.—Fishing mortalities by cohort length analysis[1] and cohort age analysis[2] by ages and different M, 1972-75[3].

Age (yr)	Cohort length analysis $M = 0.2$ F	Cohort length analysis $M = 0.3$ F	Cohort age analysis $M = 0.2$ F	Cohort age analysis $M = 0.3$ F
1	0.038	0.026	0.041	0.030
2	0.173	0.130	0.177	0.134
3	0.341	0.271	0.325	0.261
4	0.368	0.304	0.443	0.375
5	0.487	0.419	0.466	0.412
6	0.778	0.694	0.922	0.824
7	0.944	0.852	0.990	0.897

[1] Jones (1976).

[2] Pope (1972).

[3] After Skuladottir (1979).

Table 30.—Optimum temperature ranges for shrimp landings 2 yr later. (From Dow 1964.)

Month	Optimum temperature range (°C)
October	9.55 - 11.55
November	7.10 - 9.20
December	3.00 - 5.60
January	0.45 - 3.90
February	0.00 - 2.20
March	0.90 - 2.50
April	2.80 - 6.40
May	7.85 - 10.00
June	11.60 - 13.50
July	13.05 - 16.00

(1963, 1964, 1966, 1967a, 1973, 1977a, b, 1979, 1981) (section 2.3).

Fishing obviously has a great direct effect on total mortality of exploited populations of *P. borealis* (see section 5.4). The Northern Shrimp Management Plan (NSSC 1979a) for the population of *P. borealis* in the Gulf of Maine shows that the correlation between increased fishing effort and reduction in stock size is as close as the correlation between high seawater temperature and reduction in stock size. Anthony and Clark (1980) demonstrated the same close correlation between fishing effort and stock size. Horsted and Smidt (1956), Carlsson (1981), and others state that while fishing effort is high in west Greenland areas, fishing mortality does not jeopardize the stock due to the large areas of untrawlable bottom that are inhabited by *P. borealis* and protect the population from overharvesting. Most populations of *P. borealis* are protected by some form of limitation on the fishing effort (Tables 31, 32) (see section 6.1).

Table 31.—*Pandalus borealis* fishing season limitations by area.

Area	No fishing	Reason
Greenland (fjords)	Jan.-May	Ice
Iceland	Oct.-Apr.	Management
Labrador	Jan.-June	Ice
Bering Sea	winter	Ice
New England	May-Dec.	Management
Alaska	approx. Jan.-Feb.[1]	Management
British Columbia (Burrard Inlet)	Dec.-May	Management

[1] Fisheries closed for 2 mo prior to release of larvae.

Table 32.—Trawl mesh size regulations for countries under ICES management jurisdiction 1977.[1]

United Kingdom	Minimum of 16 mm cod end [under the fishing nets (N.E. Atlantic) order 1977]. Cod ends usually 25-28 mm.
Denmark	No regulations. Cod ends usually 25-28 mm.
Sweden	No regulations. Cod ends usually 35 mm.
Iceland	National regulations stipulate a 35 mm cod end. It had been proposed to increase this to 38 mm in 1979.
Greenland	Offshore fishery 40 mm cod end enforced by ICNAF. Inshore: no regulation.

[1] After ICES (1977).

An indirect effect of fishing activity on populations of *P. borealis* is the mortality of younger (smaller) shrimp that are caught in the trawls and discarded as unmarketable. NAFO (1981) documented a discard rate of 6% by weight of shrimp for a French vessel off west Greenland in 1981. Canadian data for the same general area indicated discard rates ranging from 2.4 to 7.4% in 1981 and slightly less of a range in 1980. NAFO recommended an observer program to more closely document discards.

The relationship between *P. borealis* and other species in four bays at Kodiak Island, AK, has been examined by Ippolito (1980). Species interrelationships have also been examined by Feder et al. (1978) in Cook Inlet, AK.

4.43 Factors affecting morbidity

The parasites and diseases of *P. borealis* and their cyclic nature have been reviewed (see section 3.35). The frequency of occurrence of certain parasites in *P. borealis* has been correlated with temperature in the Gulf of Maine (see section 3.35).

4.5 Dynamics of population (as a whole)

Tomlinson (1970) applied the Murphy (1965) catch equation and the dynamic pool model of Beverton and Holt (1957) to a population of *Pandalus jordani* off southern Oregon and northern California.

The generalized Murphy catch equation (Tomlinson 1970) uses age-structured catch data and an average instantaneous natural mortality rate to compute population size in numbers, instantaneous fishing mortality rates, and exploitation rates for a single cohort. Abramson and Tomlinson (1972) applied the generalized Schaefer (1957) production model GENPROD to the same stock and found close agreement with the Murphy catch equation results. A spawner-recruit relationship could not be demonstrated and thus Beverton and Holt's (1957) model with its feedback loop could not be used. A maximum sustainable yield estimate proved incorrect and a re-examination of the data by Geibel and Heimann (1976) utilizing the Murphy (1965) catch equation again found no spawner-recruit relationship. They found overriding environmental influences on recruitment and concluded that the Schaefer GENPROD model could not be used since it treated environmental input as a constant. They found that a reasonable spawning stock existed in age 1 females and that these were well protected by mesh limitations. They thus concluded that the population would fluctuate with environmental influences, but would not be hurt by fishing pressure as long as few age 1 females were caught.

Rinaldo (1976) applied two dynamic pool models to populations of *P. borealis* in the Gulf of Maine for 1966-73. The Ricker (1958) yield equation has no parent-progeny relationship and thus deals only with exploitable stock weight. The Beverton-Holt (1957) model does have a simple feedback mechanism for a parent-progeny relationship. With these models Rinaldo found the fishery had moved from optimum yield conditions in weight per recruit to a much lower figure due to increasing fishing mortality and declining age at recruitment. Rinaldo (1976, 1981) also applied GXPOPS, a generalized exploited population simulator designed by Fox (1973), to the data and obtained a reasonable tracking of the fishery.

The ICES Working Group on Assessment of Pandalid Stocks (ICES 1977) assessed *P. borealis* stocks on the Fladen ground in the North Sea, in the Skagerrak off Denmark, and in the North Atlantic off Iceland using the Beverton and Holt dynamic pool model. They found that yield in weight per recruit was very sensitive to instantaneous natural mortality (M) and recognized that no direct measure of M was possible. On Fladen, an increase of M from 0.5 to 1.0 caused yield in weight per recruit to drop 61% and on Skagerrak the same increase in M dropped yield in weight per recruit 68%. In Iceland, lower rates of M were used. An increase in M from 0.2 to 0.3 produced a 40% drop in yield in weight per recruit. The assessments showed a drop in mean selection age with a rise in M that indicated that in Fladen and in Skagerrak harvesting at maximum yield per recruit would mean harvesting the females prior to spawning. This was considered undesirable and even though the modeling suffered from unreliable input parameters, particularly natural mortality, the results indicated that a minimum mesh size should be instituted for all three fisheries to protect recruitment. The working group recommended research on: natural mortality determination; age and growth rate determination; stock identification and origin of recruitment with respect to larval distribution; and selection properties of trawl gear.

Skuladottir (1979) utilized several models in assessing maximum sustainable yield (MSY) in a *P. borealis* population in Arnarfjordur, a fjord in northwestern Iceland. She compared two least squares methods (Gulland 1961; and Fox 1975) with the catch equation method and the equilibrium yield method of Jones (1974). The catch equation method utilized the cohort length analysis method of Jones (1974) as a basis for yield per recruit and thus maximum sustainable yield (MSY). The catch equation and equilibrium yield equation proved very sensitive to the Von Bertalanffy growth parameters where slight changes in values produced large changes in MSY. Also, for lower values of natural mortality, the effort calculated by these two methods to obtain a given yield did not agree with estimates based on Gulland (1961) or Fox (1975).

Population dynamics models utilized by Abramson and Tomlinson (1972), Fox (1973), ICES (1977), Rinaldo (1976), and Skuladottir (1979) are hampered by poorly understood or unknown values for input parameters such as recruitment, age determination, growth, and natural mortality and therefore are of limited value at present to managers.

More recent assessments utilize estimates of biomass and year class strength to predict near future production and to set appropriate total allowable catches (TAC). The assessments also recommend minimum mesh sizes that allow younger shrimp to escape. Annual monitoring of a population by research surveys and obtaining catch/effort information from the fishery is necessary for these assessments.

Simulation models have been studied in Alaska by Laevastu (1978)[11] that consider the marine ecosystem to be balanced and determine the mean standing crops of various species that are required to keep the system stable.

4.6 The population in the community and the ecosystem

Squires (1970) found that in dense concentrations, *P. borealis* was present to the exclusion of other species and that as the periphery of its range was approached, a more widely mixed assemblage of species existed. Faunal assemblages have been gathered by listing of commercial by-catch, listing of the incidental catch of various species, and listing of research trawl catches.

Several authors have listed species associated with *P. borealis* on the shrimp grounds: Allen (1959), Bigelow and Schroeder (1939), Butler (1970), Fontaine (1970), Hjort and Ruud (1938), Horsted and Smidt (1956), Howard (1976), Howard and Mason (1972), ICES (1977), ICNAF (1979b), Ippolito (1980), Minet et al. (1978), Rathjen and Yesaki (1966), Ronholt (1963), Schick (1983), Smidt (1965, 1967, 1969), Squires (1965), Ulltang and Oynes (1978a, b), and Veitch et al. (1978). For a complete list of associated species see section 3.34. Abiotic factors associated with populations of *P. borealis* are discussed in sections 2.1, 2.3, 3.16, and 3.51. Recent studies by Ippolito (1980), Feder et al. (1978), and Laevastu (footnote 11) are starting to define the communities in which *P. borealis* lives in terms of the relationships between species and between the species and the environment.

5 EXPLOITATION

5.1 Fishing equipment

5.11 Gears

The otter trawl is used either as a single large trawl rig or as two small trawls almost universally in the *P. borealis* fishery. Small vessels in Alaska and Japan utilize beam trawls and a trap fishery is moderately successful in Alaska and the Gulf of Maine. At a conference on the Canadian shrimp fishery, Legare (1971) presented methods and gear utilized in the Canadian shrimp fishery and Miyazaki and Kasahara (1971) described fishing methods and gear used in Japan. Brothers (1971) compared a Japanese box trawl, a western shrimp trawl, a Yankee (semi-balloon) shrimp trawl, a small and a large shrimp sorting trawl modified from trawls used in the Gulf of Mexico, a Danish shrimp trawl, and a Japanese beam trawl in experimental work off Newfoundland and found large differences in catch. Motte and Litaka (1975) have evaluated otter trawl performance by statistical inference from the catch. Kurata (1981) reviewed Japanese shrimp gear and pointed out that otter boards are illegal in Japan and that either a beam trawl is used or the net is deployed from the boat in a circular fashion such that it remains open for a while.

Nets used for otter trawls differ from area to area. The Yankee 36 or Yankee 41 are commonly used trawls along the east coast of North America (Legare 1971), off Greenland a Sputnik trawl is common. In Iceland otter trawls with 75 to 90 ft footropes are used and in Alaska single rig otter trawls range from a 70 to a 125 ft footrope trawl and double rig otter trawls range from 60 to 100 ft in footrope dimension. The double rig otter trawl is more maneuverable than the single rig and they are hauled and redeployed more quickly. Almost every fisherman fine tunes his net roller gear and doors to fish as well as possible.

Mesh size is the prime factor in determining selection by nets. Protecting the younger year classes is universally recognized as beneficial in *P. borealis* fisheries and so a minimum mesh size is commonly a part of the regulations governing most fisheries. ICES (1977) listed minimum mesh regulations for several countries (Table 32). While ICES listed no mesh regulation for Denmark, Smidt (1981a) stated that a minimum mesh of 34 mm stretched mesh has been in force in Denmark since 1953. In the Gulf of Maine there is a minimum stretched mesh of 44.5 mm with a 6.35 mm tolerance in the cod end. Off Norway, a minimum of 30 mm was allowed south of lat. 65°N and a 35 mm minimum north lat. 65°N. Carlsson (1979) found a 20 to 22 mm mesh (knot to knot) was acceptable for Greenland waters.

Shrimp traps (pots) have been in use for a long time (Kurata 1981). McBride and Barr (1967) designed a shrimp pot that would fish in mid-water and Barr and McBride (1967) and Barr (1970a) reported on vertical migration studies using pots to catch shrimp in the water column (Fig. 45A). Bjordal (1979) examined factors affecting pot fishing for *P. borealis* off Scotland and Kessler (1969) conducted studies in tanks to test the efficiency of shrimp pots. Koike and Ogura (1977) studied the selectivity of various sizes of mesh and entrances in shrimp traps and Koike and Ishidoya (1978) estimated the behavior of *P. borealis* towards the trap. Trap fishing for shrimp has proved to be a very successful alternative fishery for the Maine lobsterman during winter when lobstering is slow (Fig. 45B). However, the trap fishery in Maine has been greatly reduced by the collapse of the shrimp stock.

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[11] Laevastu, T. 1978. Deterministic bulk biomass model for estimation of sustainable biomasses of marine ecological groups. Unpubl. manuscr., 48 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

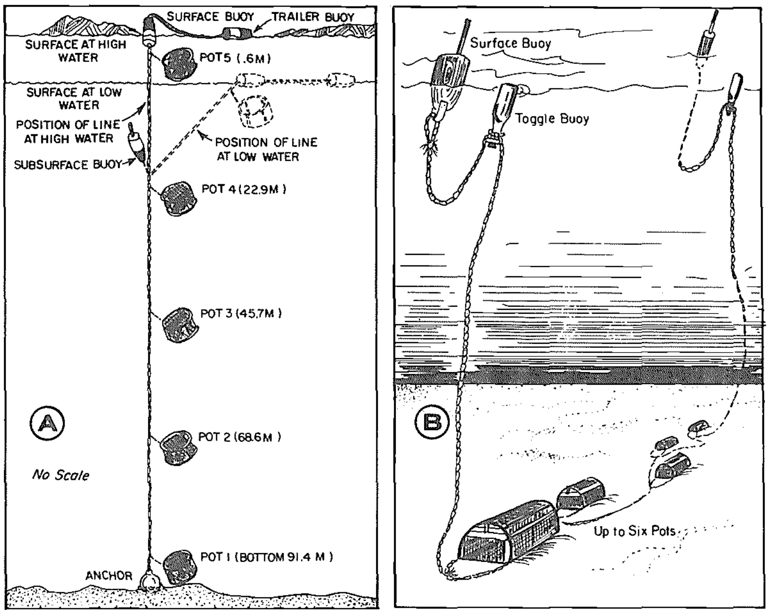

Figure 45.—Diagrammatic illustration of A) surface-to-bottom pot set to fish for shrimp (from Barr and McBride 1967); and B) typical gear conformation of Gulf of Maine pot fishery (Schick unpublished).

5.12 Boats

In his world survey of the shrimp industry, Ivanov (1964c) listed vessels participating in European shrimp fisheries. Balsiger (1981) gave a cursory description of shrimp vessels from several fisheries (Table 33). Kojima (1971) has described shrimp vessels used in the Japanese shrimp fishery and Hitz (1971) has described vessels used in the U.S. Pacific coast shrimp fisheries. Shenker (1971) has studied Canadian shrimp boat requirements, Dres (1971) designed a multipurpose fishing vessel suitable for the shrimp fishery, and Proctor (1971) has summarized electronics utilized or available to the shrimp fishery.

5.2 Fishing areas

5.21 General geographic distribution

Pandalus borealis is exploited in virtually every general area of known abundance (see section 2.1). Certain areas within the general areas have too low an abundance or the bottom is too

Table 33.—Vessel type and numbers by area. (After Balsiger 1981.)

Country	Year	Details of vessels	Remarks
Japan (offshore)	1960-67	"Eininmaru", a 7,482 GMT factory ship and others. 25 otter trawlers.	
Japan (nearshore)	1981	15-125 GMT.	
Alaska	1981	Trawler 80-100 ft keel length. 200,000-300,000 lb hold.	Double rig
		Trawler 50-70 ft up to 110 ft.	Single rig
		Trawler 25-40 ft.	Beam trawl
British Columbia	1981	Trawler prior to 1974.	Single rig
		Trawler after 1974.	Double rig
New England	1981	Trawler.	Great diversity in size
		Trapper.	Usually lobster boat
Canada:			
Labrador	1981	Freezer trawler 150-170 ft.	
Quebec	1981	Trawler 18.3 to 26.5 m.	
Greenland	1981	Trawlers.	
Iceland	1959	Displacement 7-18 tons (average 12 tons).	
	1960	30-100 hp engines (average 50-60 hp).	
	1981	Trawlers, otter 10-45 GMT.	
North Sea	1981	Trawlers.	
Skagerrak		Danish cutters 20-150 GMT.	
Barents Sea/ Spitsbergen	1981	Trawlers.	
Norway		Length 9-15 m. 20-40 hp engines.	
Sweden	1958 1960	Length 12-18 m. Old vessels have engines of about 100 hp. Modern ones: 150-200 hp. Crew of 2-4.	Fish also caught

rough for trawling and fishing is either limited or non-existent. Smidt (1965) reported the fishing area in Disko Bay, west Greenland, was limited to mud bottom but that this bottom was associated with large areas of hard bottom that hold many shrimp. Thus recruitment to the fishing area will prevent overfishing. Conversely, Haynes and Wigley (1969), Warren and Sheldon (1968), and others have associated *P. borealis* with fine grained sediment. Exploratory fishing surveys by Squires (1970) off the Canadian east coast, by Warren and Sheldon (1968) off England, by Murray (1967) off Nova Scotia, by Butler (1967) in the Gulf of Alaska and the Bering Sea, by Beals (1965) in Alaska, by Bigelow and Schroeder (1939) in the Gulf of Maine, by Butler and Smith (1968) off British Columbia, by MacPhail and MacDonald (1965) off Nova Scotia, by Rasmussen (1953) off Norway, by Rathjen and Yesaki (1966) off Alaska, by Ronholt (1963) in the northeastern Pacific Ocean, by Wollebaek (1908) off Norway, by Ivanov (1967b) in the Bering Sea and Gulf of Alaska, by Kitano and Yorita (1978) off the Kamchatka Peninsula, by Ito (1976) off Japan, and numerous other surveys have located the major concentrations of *P. borealis*. Some areas of major concentration, such as off the Pribilof Islands in the Bering Sea, have been reduced to very low levels of abundance through fishing and other areas, such as east Greenland, have shown sudden increases in abundance. The Gulf of Maine stock has shown wide fluctuations of abundance and controversy exists as to whether or not the most recent decline (mid-1970's) was precipitated solely by environmental factors or by greatly increased fishing mortality as well.

5.22 Geographic ranges

Fisheries for *P. borealis* range from within "hailing distance" of land along the Maine coast in winter to oceanic areas such as the Pribilof Islands area in the Bering Sea. In general, the fisheries are located within 100-150 nmi of shore. Most of the Alaskan fishery takes place within 12 mi of shore. The areas of greatest abundance are the North Sea, the Skagerrak off Denmark, Iceland, Greenland, Labrador Sea, Gulf of St. Lawrence, Gulf of Maine, Gulf of Alaska, and Bering Sea. Differential abundance associated with hydrographic features has been reviewed in section 2.2. The geographic range of a fishery in any one area is a function of the local abundance of the population and the opportunistic nature of the fishery in as much as the greatest effort is expended on the greatest densities of shrimp. Thus, the range of the fishery will vary as local centers of abundance are depleted or the shrimp move.

5.23 Depth ranges

Fishing depth is a function of depth of population density. Populations in general inhabit deeper water the further north they are located (see sections 2.1, 2.2, 2.3).

5.24 Conditions of the grounds

See sections 2.1, 2.2, 2.3.

5.3 Fishing seasons

5.31 General pattern of season(s)

Pandalid fisheries occur continuously in locations not influenced by environmental restriction, regulations, or local custom. There is no closed season on Fladen in the North Sea or Skagerrak off Denmark, off Norway, off eastern Canada, off Greenland, British Columbia, Bering Sea, Sea of Japan, or Sea of Okhotsk.

5.32 Dates of beginning, peak, and end of season(s)

Closures are given by area in Table 31.

5.33 Variation in date or duration of season

In northern areas, the severity of the winter will determine the start and finish of the shrimping season. Regulated closures will affect the season where applicable (see section 5.32). Laws for emergency closures in Iceland, New England, and Alaska may affect the length of season. In the Gulf of Maine, traditional fishing practices limit the Maine fishermen to an inshore winter fishery while the Massachusetts fishermen continue into the spring. The price and availability of lobsters and groundfish influence the duration of participation in the shrimp fishery. Also, during the spring, the females move back offshore and disperse, decreasing the catch per unit of effort and therefore profit to the fishermen.

5.4 Fishing operations and results

5.41 Effort and intensity

While catches are commonly documented, the effort expended to obtain the catch is not. The importance of good effort data has long been recognized as many assessment methods and population models are based on estimates of effort as well as catch. Many management schemes now require accurate logs of fishing activity as a requirement for a fishing license (Gaffney 1981). Miller and Gaffney (1981) described SYSTEM LBOOK, a computerized logbook system currently used in Alaska.

Skuladottir (1981b) reported catch and effort for two Icelandic fjords for 1956-78. Frechette and LaBonte (1981) showed the variability in the catch and effort data by month for 1977 and for annual catch and effort data for northwest Gulf of St. Lawrence for 1965-77. Jackson (1980) described the problems of obtaining meaningful effort data from the Alaskan fishery where several different vessel sizes, gear conformations, and gear types are employed in the fishery. The SYSTEM LBOOK (Miller and Gaffney 1981) attempts to deal with these problems. Effort is commonly measured as number of hours fishing where fishing means trawling time. Correlating trawling effort with effort in a trap fishery is another problem yet to be solved.

CPUE, usually given in kilograms per hour, is a measure of density. NAFO (1981) used the relative CPUE from Canadian, French, Norwegian, and Danish fisheries in west Greenland waters to help determine the stock status by showing little change between 1978 and 1981.

Year	1976	1977	1978	1979	1980	1981
Relative CPUE	1.00	0.73	0.67	0.50	0.64	0.59

5.42 Selectivity

Net conformation is important in that high rise nets have been found to catch more shrimp than semiballoon nets of the same width. Methods of assessing gear selectivity have been outlined in detail by Pope (1966). The mesh used in the cod end has traditionally been assumed to determine selectivity, or what will be retained by the net. More recently mesh size in the body and relative mesh size between the body and cod end have been found to be important (NSSC 1974). Thomassen and Ulltang (1975) reported on mesh selection experiments on *P. borealis* in Norwegian waters. ICES (1977) utilized the data from selectivity experiments conducted by Denmark, Iceland, Norway, Scotland, and Sweden to calculate a selection factor of 0.436 ± 0.016 by linear regression through the origin for mesh size (mm) versus dorsal carapace length (mm). LaBonte and Frechette (1978) found a mean selectivity of 18.6 mm dorsal carapace length for a 38 mm mesh trawl in the northwest Gulf of St. Lawrence. This agrees closely with the ICES estimate. LaBonte and Frechette (1978) found the 18.6 mm selection length equivalent to an age of 2.2 yr. ICES (1977) showed the effects of proposed increase in minimum mesh size on *P. borealis* stocks on Fladen in the North Sea, in Skagerrak off Denmark, and off Iceland in terms of increases in mean selection size and mean selection age (Table 34). This was related to size and age of first ovigerous stage to show advantages to recruitment (Table 35).

Selectivity experiments were carried out by Blott et al. (1983) to calibrate a new research trawl with 32 mm stretched mesh twine for *P. borealis* in the Gulf of Maine and the selection was essentially complete for shrimp with a 19 mm dorsal carapace length.

Table 34.—Comparison of the present mesh sizes in use and the estimated level of fishing mortality, with the proposed management recommendations for the Fladen, Skagerrak, and Iceland (Arnafjördur) fisheries for *Pandalus borealis* (from ICES 1977).

	Fladen	Skagerrak		
	Danish and Scottish fisheries	Danish fishery	Swedish fishery	Iceland
Present mesh size (mm, stretched)	25	25	35	35
Present mean selection size (carapace length-mm)	11.0	11.0	15.0	15.4
Present mean selection age (yr)	0.7	1.0	1.7	2.6
Proposed mesh size	35	45	45	38
Proposed mean selection size	15.4	20.0	20.0	16.7
Proposed mean selection age	1.5	3	3	3
Present fishing mortality (*F*)	1.0	0.7	0.7	0.3
Proposed fishing mortality (*F*)	leave same	leave same	leave same	0.4-0.5

Table 35.—Size and age when *Pandalus borealis* are first berried (= ovigerous), 50% berried, and 100% berried (from ICES 1977).

	First berried		50% berried		100% berried	
Stock	CL (mm)	Age (yr)	CL (mm)	Age (yr)	CL (mm)	Age (yr)
Fladen	15	1.4	17	1.8	19	2.4
Skagerrak	15	1.7	18	2.4	21	3.3
Iceland (Arnafjördur)	16	2.8	19	4.2	22	6.0

5.43 Catches

Some populations of *P. borealis* have shown wide fluctuations in abundance as reflected in the landings. The Pribilof Island fishery went from 0 in the late 1950's to 30,000 t (metric tons) in 1963, then dropped to < 10,000 t in 1965 and then dropped to 220 t by 1972. In the Gulf of Maine, an equally dramatic collapse occurred in the mid-1970's (Fig. 46). Catches by the major fisheries for *P. borealis* are given by Balsiger (1981) (Table 36).

The concept of maximum equilibrium yield is difficult to embrace for an organism that shows such wide fluctuations in abundance.

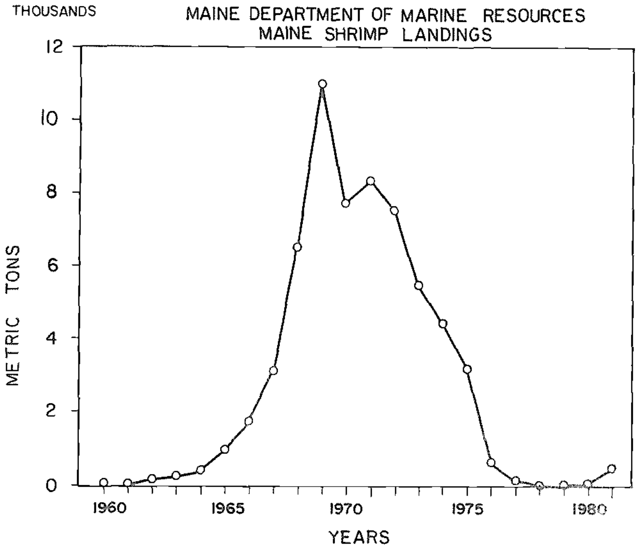

Figure 46.—Commercial Maine landings of shrimp (*Pandalus borealis*) during 1960-80 in thousand metric tons.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.11 Limitation or reduction of total catch

Limiting total catch involves either setting a quota, or setting a season, or limiting effort by controlling the number of fishermen (limited entry), or controlling the efficiency of fishing.

In the northwest Atlantic, shrimp are managed by a joint agreement of the European Economic Community and Canada. Research surveys are carried out by member countries and assessments of the stocks are conducted by the Standing Committee on Fishery Science of NAFO. Recommendations are made to the member countries as Total Allowable Catches for each area considered.

Alaska sets quotas by area as does Iceland, but Iceland reassesses and revises estimates half way through the season.

In Canada, the effort is limited by controlling the number of fishermen, while in the Gulf of Maine effort is limited by a closed season. In Japan, the efficiency of the gear is limited in coastal areas by outlawing otter trawls.

6.12 Protection of portions of population

Alaska closes the fishery for a 2-mo biological protection period prior to larval release. Many fisheries protect younger shrimp with a minimum mesh size (see section 5.42). Management of the fishery in the Gulf of Maine provides a minimum

Table 36.—Pandalid shrimp catches by area in metric tons, heads on.

Year	Washington-California[1]	British Columbia[2]	Alaska[1]	Bering Sea[3]	New England[1]	Canada east coast[2]	Greenland[4]	Iceland[4]	Barents Sea[4]	Spitsbergen/ Bear Island[4]	Norwegian Sea[4]	North Sea and Skagerrak[4]
1961	2,240	550	7,250	14,120	30	—	2,545	1,375	835	—	2,910	13,930
1962	2,700	755	6,685	18,390	175	—	3,365	—	500	—	3,500	16,590
1963	2.780	810	6,860	29,540	255	—	3,340	—	335	—	3,315	17,900
1964	3,070	475	3,505	20,880	420	—	3,770	675	360	—	3,325	15,590
1965	1,485	795	7,630	9,765	950	—	5,050	900	665	—	4,075	14,635
1966	2,835	765	12,790	2,935	1,765	—	5,380	1,790	985	—	3,925	9,050
1967	5,735	770	18,960	3,300	3,170	570	5,650	1,510	1,185	—	4,365	8,650
1968	6,500	710	19,085	12,735	6,610	1,015	5,605	2,450	940	—	3,570	9,925
1969	6,620	960	21,680	9,505	12,820	1,141	6,740	3,275	1,500	—	3,090	9,020
1970	8,485	700	33,725	6,155	10,645	2,020	8,560	4,510	2,115	290	3,105	9,100
1971	5,915	335	42,670	2,855	11,130	1,780	9,440	6,325	2,280	315	2,550	10,440
1972	10,930	360	39,330	220	11,095	1,385	9,530	5,290	2,985	1,070	2,720	8,775
1973	14,140	785	51,805	155	9,405	2,170	12,640	7,285	1,645	2,460	2,815	6,570
1974	14,340	1,200	48,756	105	7,945	3,520	22,010	6,515	1,345	3,120	4,530	5,250
1975	17,680	785	44,900	3,555	6,135	4,710	37,890	4,940	60	5,160	2,980	6,730
1976	17,235	3,505	58,520	2,205	1,665	5,015	49,675	6,450				
1977	34,010	2,765	53,030	615	365	—						

[1] From *Fisheries of the United States*, U.S. Department of Commerce.

[2] From *Annual Statistical Review of Canadian Fisheries*, Vol. 9, Fisheries and Canada.

[3] From *NPFMC Bering Sea Shrimp FMP*, draft manuscr., and refers only to Japanese harvests.

[4] From *Bulletin Statistique des Peches Maritimes*, ICES.

mesh size, but does little to protect the larvae as it directs the fishery at the ovigerous females by limiting the fishery to a winter season.

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