On the Biology of an Intertidal Chthamalid (Crustacea, Cirripedia) from the Chukchi Sea

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ABSTRACT. The Pacific-Boreal species *Chthamalus dalli* occurs intertidally near Cape Thompson, Alaska. Other organisms, apart from ephemeral algae, are absent from the intertidal zone, and the barnacle apparently survives the winter frozen in the ice-foot. From annual rings on the shell growth appears to be less than in southern localities, but continues for five years or more: maturity is reached in two years and breeding can occur at a sea-temperature of 6°C. Curves of cirral activity plotted against temperature show only slight lateral shift (cold-adaptation) compared with the same species from southeast Alaska and southern California.

The absence of the Boreo-arctic species *Balanus balanoides* is discussed, and it is concluded that the longer summer breeding period of *C. dalli* may have given it an advantage over *B. balanoides* in colonising the Eastern Chukchi Sea under existing hydrographic conditions.

RÉSUMÉ. *Sur la biologie d'un chthamalide intertidal* (*Crustacea*, *Cirripedia*) *de la mer de Tchoukotsk.* Près du cap Thompson, Alaska, on trouve dans la zone intertidale l'espèce pacifique-boréale *Chthamalus dalli.* A part quelques algues éphémères, les autres organismes sont absents de la zone intertidale: la cirripède en question passe l'hiver gelée dans le pied-de-glace. La croissance, étudiée sur les anneaux de la coquille, semble plus lente que dans des localités plus méridionales, mais dure cinq ans ou plus: la maturité est atteinte en deux ans et la reproduction a lieu à une température de l'eau de mer de 6°C. La comparaison entre les courbes de l'activité cirrale et de la température montre un léger déplacement latéral (adaptation au froid) par rapport à la même espèce dans le sud-est de l'Alaska et le sud de la Californie.

Les auteurs discutent de l'absence de l'espèce boréale-arctique *Balanus balanoides* et concluent que pour les conditions hydrographiques existantes, la période de reproduction estivale plus longue chez *C. dalli* a pu lui donner un avantage sur *B. balanoides* dans la colonisation de l'est de la mer de Tchoukotsk.

РЕЗЮМЕ. *О биологии морских желудей* (*Crustacea*, *Cirripedia*) *приливно-отливной зоны Чукотского Моря.* Тихоокеанско-бореальный вид *Chthalamus dalli* встречается в приливно-отливной зоне около мыса Томпсон, Аляска. Иные организмы, кроме эфемерных водорослей, здесь отсутсвуют, а морской желудь очевидно переживает зиму вмерзший в береговой лед. Судя по годовым кольцам на раковине рост здесь медленнее, чем в южных областях, но продолжается пять лет или больше; зрелость достигается в два года, а размножение может происходить при морской температуре в 6°Ц. Кривые циррусовой деятельности, сопоставленные с температурой, показывают лишь незначительный боковой сдвиг (адаптация к холоду) по сравнению с тем же самым видом в Юго-Восточной Аляске и в Южной Калифорнии. Отсутствие бореально-арктического вида *Balanus balanoides* заставляет притти к выводу, что более долгий летний период размножения *C. dalli* дает этому виду преимущество над *B. balanoides* в колонизации восточной части Чукотского моря при существующих гидрографических условиях.

During the University of Washington surveys of the eastern Chukchi Sea in 1959 Professor R. H. Fleming and his associates collected some barnacles belonging to the genus *Chthamalus* on a slab of rock from the shore near Cape Thompson, Alaska (Fig. 1). This find was very surprising, since Zenkevitch (1963) had reported the absence of intertidal organisms in the Chukchi Sea, and the genus is mostly restricted to warm water. In fact only three species of *Chthamalus* are known to penetrate the north temperate area. *Chthamalus fragilis*, which is apparently of tropical origin, occurs along the west side of the Atlantic to just around Cape Cod (personal communica-

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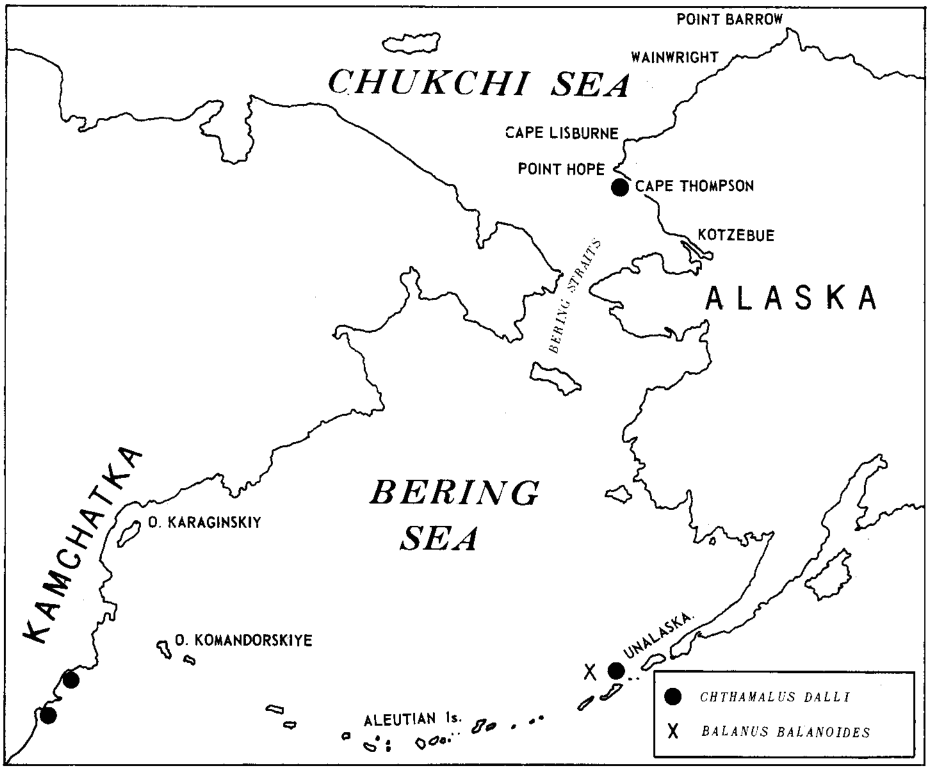

FIG. 1 The known distribution of *Chthamalus dalli* and *Balanus balanoides* in the Bering Sea and Chukchi Sea, showing other localities mentioned in the text. It is possible the species actually occur further north in the Bering Sea than shown here.

tions; D. J. Crisp and V. Zullo). *Chthamalus stellatus* is also a straggler from warmer waters, and occurs along the eastern side of the Atlantic as far north as the Shetland Islands (Southward and Crisp 1956). The third species, *C. dalli*, is somewhat more of a cold water form than the other two, and it is apparently to this species that the Chukchi Sea specimens belong. Hitherto *C. dalli* has been recorded only as far north as the Aleutians and S. E. Alaska (Pilsbry 1916; Henry 1942) and the southwest Bering Sea (S. E. Kamchatka, but not Karaginskiy or Komandorskiye islands; Tarasov and Zevina 1957; Spassky 1961).

The Cape Thompson discovery extends the species a good deal to the north of these records and it was felt that further researches would be worthwhile. The Arctic Research Laboratory sub-station near Cape Thompson was therefore visited in July 1963, and a good sample of the barnacles collected. The material was taken alive to Point Barrow, where experiments were carried out on the relationship between temperature and cirral activity, and some general biological observations were made. The results are reported here and compared with what is known of the species from further south and with reported occurrences of other species of barnacles on the shore in the arctic regions. The exact taxonomic status of the Cape Thompson material is being determined by Dr. Dora Henry.

ENVIRONMENT

At Cape Thompson the sea ice forms in October and a solid ice foot (or ice and gravel 'kaimoo') persists throughout the winter until the spring breakup begins in late May (personal communications: R. Kachadoorian and H. Smith; cf. Hicks and La Fond 1959). On 20 July we found slight traces of the ice foot still present on some shaded parts of the beach above the normal limit of wave action. At that time the sea temperature inshore was 6.7°C. and the salinity 30.8$^0/_{00}$. From Fleming *et al.* (1961) it appears that the surface water close to Cape Thompson reaches a maximum of 11.0 to 11.5°C. (salinity 28.5 to 30.4$^0/_{00}$) in mid-August, while the deeper water below the thermocline remains at 6.0 to 8.5°C. (31.5$^0/_{00}$). The surface water can reach somewhat higher temperatures further east in the Chukchi Sea, for example 13°C. at the entrance to Kotzebue Sound, but it is cooler to the west, reaching only 10°C. at Point Hope and Cape Lisburne, and declining to 7°C. at Wainwright. These figures may be compared with the observations we made close to the beach at Point Barrow, during part of our stay there (observations on fifteen days in the period 20 July to 10 August; temperature, mean 1.24°C, range −0.8 to 4.0°; salinity, mean 27.8$^0/_{00}$, range 25.0 to 32.0$^0/_{00}$. Obviously conditions at Cape Thompson are not truly arctic, nor are they representative of the Chukchi Sea (cf. Zenkevitch 1963) but they are more severe than the barnacle would experience in the southern Bering Sea. The relative warmth of the eastern Chukchi Sea in summer appears to be due in part to the flow of water that then passes north through the Bering Straits (Zenkevitch, 1963). Recent hydrographic evidence indicates that this flow tends close toward the Alaskan side (Coachman and Barnes 1961) as would be expected from the effects of Coriolis force, and this is confirmed by drift bottle experiments which indicate a rate of flow of 6 to 12 miles a day, occasionally more (Fleming and Hegarty 1962). In summer the north-going flow of Bering Sea water is warm, though of low salinity; in winter it is more saline (up to 34.0$^0/_{00}$) but near freezing point (Coachman and Barnes 1961).

The tidal range near Cape Thompson is very small (approx. 0.25 m.), and changes in water level due to meteorological effects are often more important than tidal changes (personal communication: R. Kachadoorian; cf. Hunkins 1965). Wave action is obviously important in maintaining an 'intertidal zone' under these conditions (cf. Southward 1958). During our brief stay in the district up to 0.6 m. of swell and wash was seen with a light southeasterly breeze blowing along shore. From local meteorological observations (personal communication: R. Kachadoorian) it appears that during the ice-free period from May to October the wind blows onshore (directions from SE. to W.) for nearly 60 per cent of the time, at an average velocity of 15 knots. Hence the wave action we observed is probably normal.

Presumably the ice foot is formed mainly by wave action, and must cover most of the narrow tidal zone (cf. conditions in Greenland and Spitsbergen; Feyling-Hanssen 1953a; Høpner Petersen 1962).

OCCURRENCE

We found the barnacles about 1 mile west along the beach from the substation at Ogotoruk Creek (68° 06′ N., 165° 46′ W.), at the foot of a nearly vertical cliff called Crowbill Point (see detailed map and photographs in Sainsbury, Kachadoorian, Campbell, and Scholl 1965). The foot of the cliff was covered by a pile of large slabs of rock fallen from the cliff, and at least a few metres deep; they appeared to be free of any soil or gravel infilling. The barnacles were present on the seaward slabs of the pile, from about 0.3 m. below the level of the sea at 20.00 h. (150° meridian time) on 19 July 1963, up to about 0.1 m. above the level of the sea, and were alternately covered and exposed by the waves: as far as can be judged from imperfect tidal data, this level corresponds to about mean lower low water, or zone 3 of Ricketts and Calvin (1962). The barnacles were not at all easy to see, and were mostly on the sides and underneath of the slabs, particularly where the surface was pitted and eroded. Several counts made on the largest piece of rock collected gave the following mean population densities: larger individuals (2-yr. and more old) 0.2 per $cm.^2$; smaller individuals (1-yr.-old) 0.5 per $cm.^2$ (see *Growth*, below). Most specimens were isolated, and crowding occurred only in pits and depressions.

No other animal was found, and the only plants seen were diatoms and filamentous green algae which, with trapped silt particles, formed a green-brown fuzz over the rocks. Searches were made by boat along the cliffs towards Cape Thompson itself, but although landings were effected at several places no more barnacles or other animals were seen.

BREEDING

In a subsample examined and preserved on 22 July, after return to Point Barrow, approximately 54 per cent of the 2-yr.-old *Chthamalus* were incubating nauplii, and others were judged to have liberated their larvae recently. Some of the specimens being examined for rate of cirral activity attempted to copulate even at 4°C.; this indicates that low temperature is little handicap to fertilization of the eggs, and suggests that more than one brood is produced during the summer, as is usual in other *Chthamalus* (Crisp 1950; Crisp and Davies 1954).

GROWTH

The large specimens all showed obvious growth marks on their shells, similar to those noted in *Balanus balanus* (Crisp 1954), indicating that the

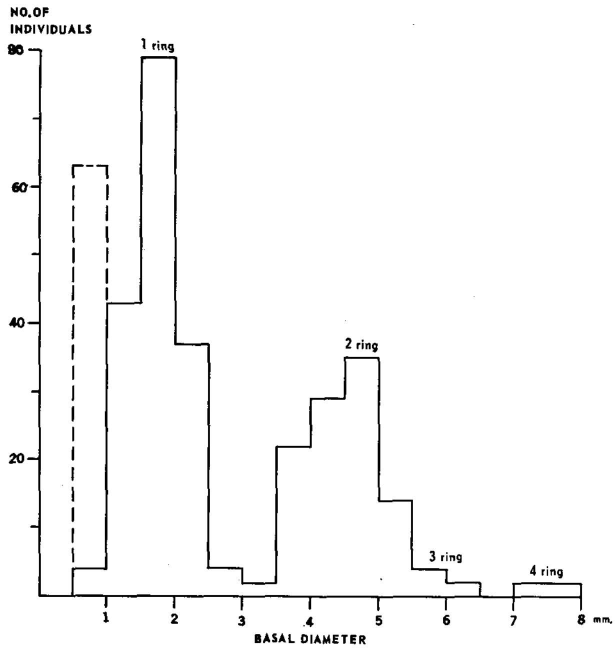

FIG. 2 Size-frequency data for *Chthamalus dalli* from near Cape Thompson, July 1963. The broken lines refer to small empty shells which are presumed to have died during the winter.

adults successfully survived the winters to grow again in subsequent summers. Measurements of the shell diameter of a subsample of 280 individuals showed at least three age groups (Fig. 2). The smallest living specimens, with a mode of 1.6 to 2.0 mm. bore 1 growth ring on the shell, and are presumed to have settled the previous summer. The size reached by this group at the end of the first summer can be estimated (0.6 to 1.0 mm.) from the very small dead shells also present, which probably died before growth began again in the spring. The second group, mostly 2-ring shells with a mode at 4.5 to 5.0 mm., overlapped slightly with a small group of 3-ring specimens. The few specimens in the 7.0 to 8.0 mm. groups bore at least 4 rings on the shell, but from the sizes of these rings, they were probably older, the first-year rings having been removed by erosion of the shell at the apex. Such an exceptionally old specimen is illustrated in Fig. 3 together with the more normal ages.

The probable rate of growth, based on the rings and the measurements is as follows:

age from settlement	3 mo.	1 yr.	2 yrs.	3 yrs.	4 yrs.	5 yrs. and over
mean basal diameter mm.	0.8	1.8	4.5	5.5	6.5 (estimated)	7.5

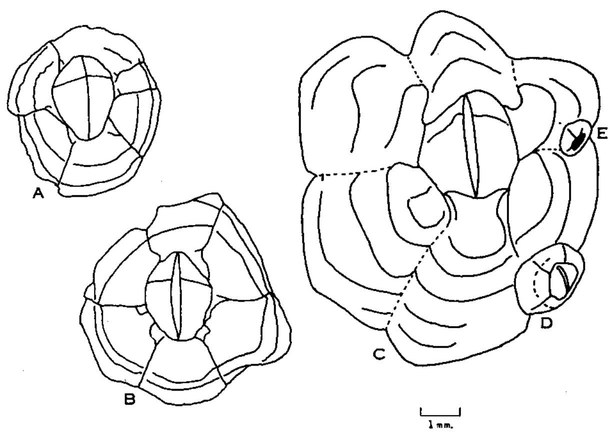

FIG. 3 *Chthalamus dalli* from near Cape Thompson, July 1963. A. 2-ring specimen; B. 3-ring individual with first ring eroded away; C. very old individual, over five years old; D. 1-ring 'spat'; E. dead shell of 1962 settlement.

Either the settlement occurring in 1961 experienced unusually favourable conditions or else most growth occurs in the second summer from settlement.

There is a dearth of comparable growth data on *C. dalli* from other localities. From the specimens in our own collection we deduce that a basal diameter of 4.3 to 5.5 mm. can be reached in one year at low water levels on the open coast of Vancouver Island, and about 6.0 mm. the second year. Worley (1930) notes that the species may reach 7.5 mm. in Puget Sound. Adult high-water individuals along the Pacific Coast are obviously several years old, and being crowded together grow more in height; they usually achieve a basal diameter of at least 5 mm. On the western side of the Pacific it is not at all clear to what extent the distribution of *C. dalli* overlaps with the southern form *C. challengeri*: Kato *et al.* (1960) report that specimens of the latter species from Mutsu Bay, N. Honshu, show growth rings on the shell, and we interpret their morphological data as showing a basal diameter of 5 mm. at two years in low water specimens, while older, high-water individuals reach 6 to 7 mm. at the end of four years.

The rate of growth at Cape Thompson is therefore a little less, during the first two years, than in more temperate regions. However, growth continues more or less unchecked, and in later years the rate is higher and the ultimate size reached is greater than in more southern localities. An increase in maximum size with increase in latitude is a well-known zoological phenomenon also found in *Balanus balanoides* (Moore 1934).

BEHAVIOUR

The frequency of beating of the cirri was determined at a number of temperature points by the technique used previously (Southward 1957, 1962). Small pieces of rock bearing the barnacles were placed in a long Perspex trough with a central division. Sea water was circulated round the trough by an enclosed paddle wheel, the velocity of the flow being adjusted to produce the maximum number of specimens active. Relatively warm, saline water (4.0°C., 32.0$^0/_{00}$) was present along Barrow beach at the time and this was used directly for the experiments, which were carried out in an insulated portable wooden hut ('wanigan'). The temperature in the hut could be maintained at 4 to 5°C. by varying the ventilation, and the barnacles were normally kept at this level. The temperature of the water in the experimental trough was altered by means of a small immersion heater or with beakers of ice and salt. The rate of change of temperature was limited to 5° per hr., and each temperature point represents the mean of a sequence of observations made over a range of 0.2 to 0.5°. At each temperature level the time taken for ten beats of the cirri was noted for at least ten specimens, and then converted to beats per 10 sec. Only the 2-ring specimens were used, as there were insufficient older individuals, and the young 1-ring specimens would not beat regularly enough, tending to hold the cirri stiffly even in a slight flow of water (the extension response, Crisp and Southward 1961).

The main results are shown in Fig. 4. Some activity was observed at the lowest temperature achieved (−1.1°; at −1.5° ice crystals in the water jammed the paddle wheel). The mean rate increased linearly up to 20°C., and reached a maximum at 25°C. Beyond this temperature the rate declined in a smooth curve until all activity ceased at 35.5°C. It is obvious that these specimens of *Chthamalus* were living at the lower end of their temperature/cirral activity curve at Cape Thompson, the actual temperatures experienced there (at least −2° up to 11.5°C.) being very much less than the range for activity, and well below the optimum level (25°C.).

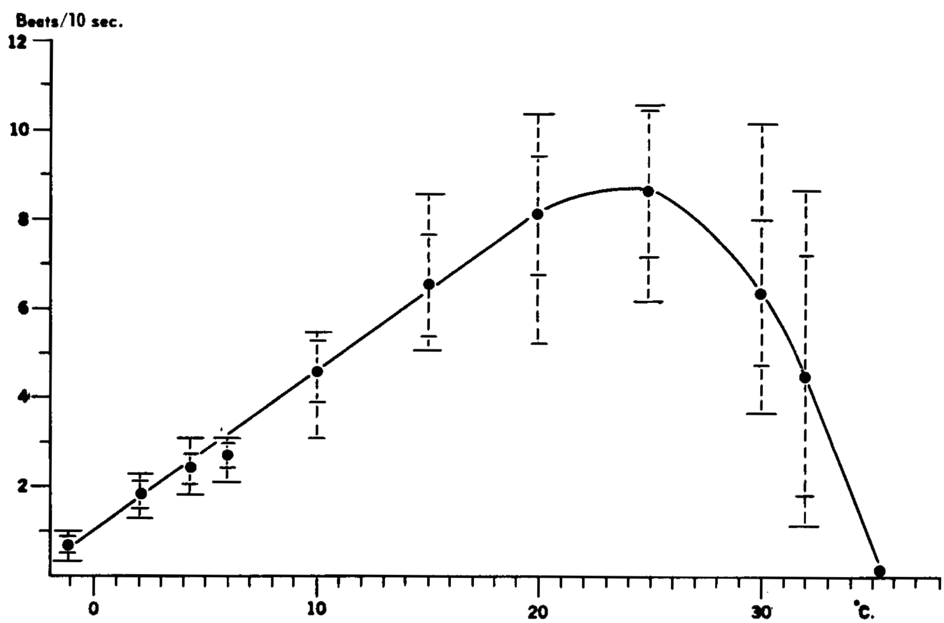

FIG. 4 Rate of cirral beating of *Chthamalus dalli* from near Cape Thompson, July 1963. The black circles and heavy line show the mean rate; the smaller cross lines at each temperature point show one standard deviation each side of the mean, and the longer cross lines show the range. The open circle indicates cessation of activity.

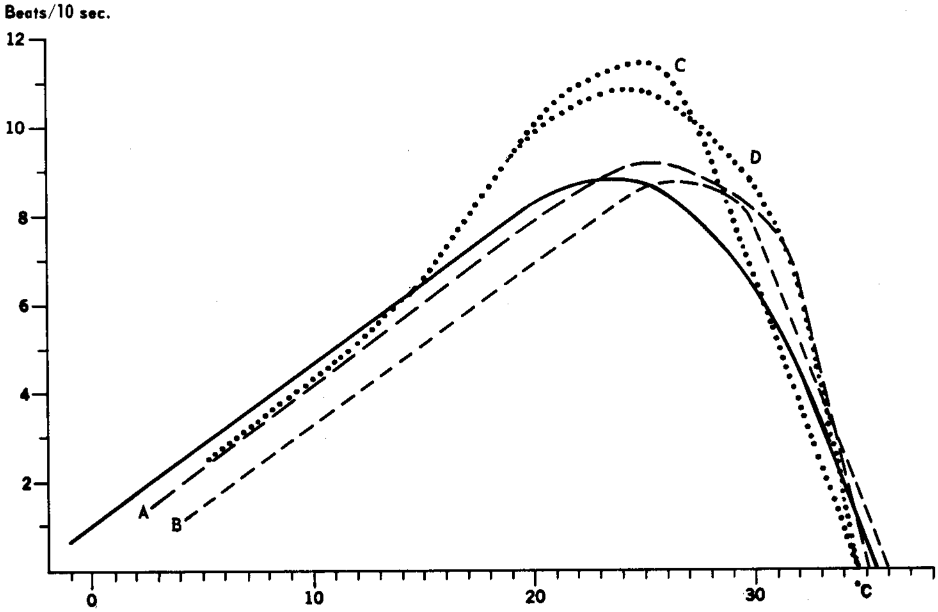

FIG. 5 Mean rate of beating of the cirri of *Chthamalus dalli* from five localities. Solid line: near Cape Thompson; A. from H. W., Puget sound; B. from H. W., Sitka; C. from L. W., Malibu; D. from L. W., Sitka.

Fig. 5 confirms how little these barnacles were adapted to life in the Subarctic. Compared with corresponding curves determined on *Chthamalus dalli* collected at several localities along the Pacific coast, the mean rate of the Cape Thompson specimens shows only a slight lateral shift, amounting at the most to 2°C. Statistically these differences are not significant ($P>0.1$), especially those at 25-30°C., where there is a great individual variation in tolerance of high temperature.

It is worth noting that good agreement is shown between the Cape Thompson barnacles and those from high water levels in Puget Sound and at Sitka. There is much less agreement with the low water specimens from Sitka and Malibu, and the differences at the optimum temperature are quite significant ($P<.001$). This suggests that the level on the shore occupied by *Chthamalus* in the almost tideless Chukchi Sea corresponds ecologically with the high water habitat in places with a greater tidal range.

DISCUSSION

In other parts of the Arctic, or more correctly, the Subarctic (Dunbar 1947), where barnacles occur intertidally, for example in Spitsbergen (Feyling-Hanssen 1953*b*) and West Greenland (Høpner Petersen 1962), the species is *Balanus balanoides*. This boreoarctic form is usually accompanied by other intertidal organisms, notably *Fucus* and *Littorina saxatilis*, though the latter may also occur alone beyond the northern limit of the barnacle.

According to Madsen (1936, 1940) *Littorina* escapes the winter freeze-up by migration into the sublittoral; Høpner Petersen (1962) puts forward evidence to suggest that it survives in crevices covered by the ice foot at about mean high water and migrates up and down the shore after the ice melts. Feyling-Hanssen (1953*b*) has suggested that *Balanus balanoides* likewise survives the winter in crevices frozen in the ice foot, but this view has been challenged by Høpner Petersen (1962) who notes that the ice foot in West Greenland does not extend below mean tide level, yet the barnacle survives at levels below this. However, *B. balanoides* is obviously more abundant in West Greenland than in Spitsbergen, and it may be that ice action is less severe there. All these authors do agree that the main factor limiting northward extension of *B. balanoides* is the length of the ice-free season, which must last long enough for the planktonic larvae to grow and then metamorphose (see also, Barnes 1957*a*). The habitat at Cape Thompson would appear to be quite favourable by these criteria: there is an ice foot in winter and, in summer, an ice-free period of several months during which the temperatures are at least comparable with if not higher than those of West Greenland. Therefore, it is not the presence of a barnacle on the shore that is unusual at Cape Thompson, but the fact that it is a *Chthamalus* and is not accompanied by any other intertidal animals.

It has been shown elsewhere (Southward 1955; 1964*b*) that *Balanus balanoides* is a cold-adapted form: specimens from England and Southeast Alaska are comparable in cirral behaviour, and reach their optimum activity at only 15 to 18°C. On a purely temperature basis, therefore, *B. balanoides* is better fitted for life in the Chukchi Sea; yet, according to Tarasov and Zevina (1957), it does not occur north of the Bering Straits, and we have been unable to find any published records north of the Aleutian chain (see Fig. 1). In fact, on the American side of the north Pacific *B. balanoides* has been correctly recorded only for Unalaska and Sitka (Pilsbry 1916; Henry 1942 and personal communications), to which we can add Douglas, near Juneau. Feyling-Hanssen (1953) and Barnes (1957) quote Shelford (1930) as their authority for the occurrence of *B. balanoides* on the eastern side of the Bering Straits. Unfortunately there is no trace of this record in the paper quoted, nor in other papers by Shelford and his co-workers (see for example Shelford *et al.* 1935). Indeed Shelford states plainly that he examined localities from Skagway to San Diego, and apparently did not visit any part of the Bering Sea. There is an amazing dearth of information on the intertidal zone of the Bering Sea, apart from the Russian work in southeast Kamchatka already quoted.

There are other factors to consider besides temperature: (1) the tidal range is very small and the intertidal zone at Cape Thompson is probably comparable to that of the Baltic and Mediterranean Seas; (2) the locality is a long way from the nearest other recorded habitats for either *B. balanoides* or *C. dalli*, and on the eastern side there are long stretches of intervening coast-line without rocky substrata suitable for barnacles. The tidal factor is probably less important than it at first appears: *B. balanoides* can form a narrow zone in almost tideless areas around the entrance to the Baltic, provided that the salinity is high enough, as for example at Elsinore and the Bohuslan coast (personal observations; Barnes and Barnes 1962), though it is a *Chthamalus* that forms the real barnacle zone in the tideless Mediterranean (cf. Southward 1964*a*). There is no reason to suppose the salinity is too low for *B. balanoides* at Cape Thompson, since we found it thriving in the normal intertidal zone of the Juneau area of southeast Alaska, where the summer salinity is less than $20^0/_{00}$. Of course, the effects of ice action and fluctuating salinity may be accentuated by the small tidal range, but this would be more likely to account for the lack of other intertidal animals than the occurrence of one barnacle and not another.

The probable discontinuous nature of the intertidal barnacle populations may well be the most important factor governing their distribution in the Bering and Chukchi Seas (cf. Crisp and Southward 1953, 1958). *Balanus balanoides* differs from *Chthamalus* in producing only one brood of young a year. Although the Alaskan population has not been examined in this respect, on both sides of the Atlantic the developing eggs are retained in the parent shell during the winter and the larvae are liberated in the spring, often in synchrony with the local outburst of plankton (Barnes 1957*b*, 1962; Crisp 1959; Rzepishevsky 1962). The evidence presented here indicates that even at Cape Thompson *Chthamalus* produces at least two broods, and it is probable that more broods occur further south where the breeding season may last several months (cf. Crisp 1950). Let us consider a situation in which the shores of the Chukchi Sea (and possibly most of the Bering Sea) were devoid of life following a postglacial climatic minimum. The Pacific population of *B. balanoides*, presumed to have been continuous throughout the Arctic with that of the north Atlantic during a postglacial climatic optimum (Feyling-Hanssen 1953), would have been completely isolated, as it still is today, and thus any recruitment of intertidal barnacles into the Chukchi Sea could only occur from the south. There is a rapid change of climate when passing north from the Aleutians and the single brood of larvae produced by *B. balanoides* in the south may well be liberated before the spring breakup of ice in the Chukchi Sea. Consequently, larvae carried in the north-going current would be unable to settle, and thus its own breeding arrangements might effectively limit any northward recolonisation by *B. balanoides*. In contrast, some of the multiple broods of *Chthamalus* must be liberated in late summer when the Bering and Chukchi Seas are free of ice, and the larvae should be able to take advantage of the northward flow of warm water to reach new habitats. Once settled, the survival of the *Chthamalus* would be assisted by the absence of some of the predators found further south (e.g. *Thais*, *Pisaster*), and the only real obstacle to their establishment would be an inability to withstand the winter. We are convinced that the presence of an ice foot is important in ensuring the over-wintering of intertidal life in the Arctic. Even if the ice foot does not directly cover the whole intertidal zone, as in West Greenland, its presence down to mean tidal level will act as a fender against ice pressure and will keep off all but the smallest ice fragments during the critical periods of freeze-up and thaw when the pack is moving alongshore.

The occurrence of *Chthamalus* in the Chukchi Sea does not affect previous conclusions as to the marine zoogeography of the area based on the benthic fauna. The Bering and Chukchi Seas contain Pacific-boreal, boreoarctic and high arctic species (Filatova and Barsanova 1964; McLaughlin 1963) but the eastern side has a greater preponderance of boreal forms, some of which extend to Point Barrow and the Beaufort Sea (MacGinitie 1950; personal records). Sparks, Pereyra, and Ellis (1961) report that in the shallow water off Cape Thompson high arctic species are almost absent; they believe the northgoing flow of water acts as a physical barrier to the spread of larvae of species living to the north. We would suggest however that the comparatively high summer temperature in the eastern Chukchi Sea may be sufficient to exclude high arctic stenotherms, and must certainly encourage the survival and breeding of the boreal forms, including *Chthamalus.*

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