Helgoländer wiss. Meeresunters. 20, 346–359 (1970)

Cultivation of *Calanus helgolandicus* under controlled conditions

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KURZFASSUNG: **Kultivierung von *Calanus helgolandicus* unter kontrollierten Bedingungen.** Der planktonische Copepode *Calanus helgolandicus* (Calanoida) wurde im Labor vom Ei bis zum Adultus in bewegten Kulturen bei 15° C aufgezogen. Die kettenbildenden Diatomeen *Chaetoceros curvisetus, Skeletonema costatum* und *Lauderia borealis* sowie der Dinoflagellat *Gymnodinium splendens* wurden als Nahrung angeboten. Die Nahrungskonzentrationen, die zum Teil den Phytoplanktonkonzentrationen im Pazifischen Ozean an der Küste Südkaliforniens entsprachen, lagen zwischen 28 µg und 800 µg organischem C/l. In Abhängigkeit von Nahrungsqualität und Nahrungskonzentration wurden folgende Ergebnisse erzielt: Die Mortalität von *C. helgolandicus* während der gesamten Entwicklung vom geschlüpften Nauplius bis zum Adultus lag zwischen 2,3 % und 58,2 %. Die Zeitspanne vom Schlüpfen bis zum adulten Stadium währte 18 bis 54 Tage. Das Geschlechterverhältnis in verschiedenen Kulturen im Labor aufgezogener Tiere schwankte erheblich. Der höchste Prozentsatz von ♂♂ (ca. 25 %) wurde erhalten, als *L. borealis* beziehungsweise *G. splendens* gefüttert wurden. Die Länge der ♀♀ stand in direktem Verhältnis zur angebotenen Nahrungsmenge und lag zwischen 3,03 mm und 3,84 mm. Im Labor aufgezogene und befruchtete ♀♀ legten durchschnittlich 1991 Eier pro ♀ bei einer Schlüpfrate von 84 %. Spermatophorentragende ♀♀ aus dem Pazifischen Ozean legten durchschnittlich je 2267 Eier, die eine Schlüpfrate von 77 % aufwiesen. Die Ergebnisse beweisen, daß es möglich ist, *Calanus helgolandicus* ohne Schwierigkeit im Labor aufzuziehen. Sie zeigen, daß die Nahrung (Diatomeen und Dinoflagellaten) bei verschiedenen natürlichen Konzentrationen auf Wachstum und Mortalität der larvalen Stadien einen starken Einfluß ausübt.

INTRODUCTION

Species of the genus *Calanus* (Copepoda, Calanoida) are common representatives of the zooplankton in the marine environment. As the larval and adult stages are a main link between phytoplankton and fishes – such as sardine, anchovy and herring – *Calanus* appears to be a rather important link in the marine food chains.

MULLIN & BROOKS (1967, 1968) extended our knowledge on the interconnections between phytoplankton and *Calanus helgolandicus*, the dominant herbivorous copepod in the Pacific Ocean off La Jolla, USA, by correlating observations from the ocean with those made in the laboratory.

A new culture method for copepods and the use of chain-forming diatoms and dinoflagellates made a new approach possible: the cultivation of *Calanus helgolandi-*

cus at natural food concentrations. In the Pacific Ocean off La Jolla chain-forming diatoms and dinoflagellates are represented in most of the phytoplankton populations. In the waters off La Jolla *Chaetoceros curvisetus* is often one of the dominating phytoplankton species; *Skeletonema costatum* occurs frequently, while *Lauderia borealis* is less common. As we were unable to culture members of the dominant dinoflagellate genus *Peridinium, Gymnodinium splendens,* which occurs mostly in sporadic blooms, was chosen.

These four species were offered in continuous cultures at different concentrations to *C. helgolandicus* throughout its entire development, in order to evaluate their influence on (1) the length of the period from hatching to adulthood (days), (2) mortality (during the same period), (3) size of adult females and (4) sex ratio. Furthermore the fecundity of *C. helgolandicus* females, raised and fertilized in the laboratory, was compared with that of spermatophore carrying females caught in the ocean.

MATERIAL AND METHODS

Fertilized *Calanus helgolandicus* females were collected 3 to 5 km offshore from Scripps Institution of Oceanography, La Jolla. They were kept at 15° C in 1000 ml-beakers filled with filtered seawater and were fed the diatom *Lauderia borealis.* The beakers were checked at least once per day and the eggs laid transferred to separate beakers.

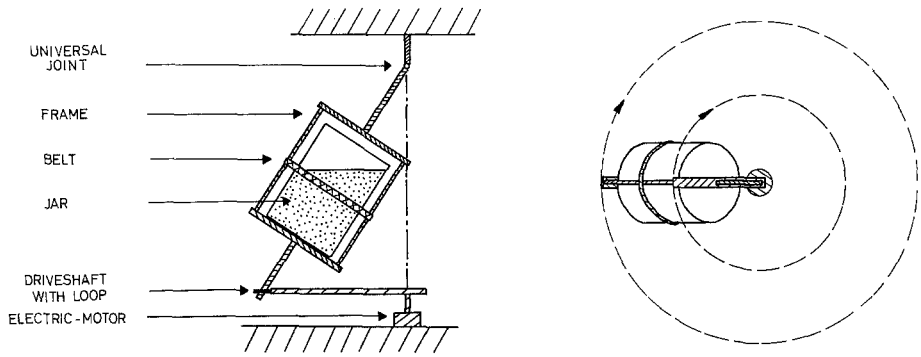

Fig. 1: Culture apparatus. Left: side view. Right: viewed from above

The chain-forming diatoms *Chaetoceros curvisetus, Skeletonema costatum, Lauderia borealis* and the unarmoured dinoflagellate *Gymnodinium splendens* were offered separately at concentrations ranging from 28 μg to 800 μg organic C/l. These algae were grown at 15° C in 2800 ml Fernbach-flasks filled with 1300 ml of filtered seawater and exposed to a light-dark cycle of 14 h light and 10 h darkness. The algae always grew in double filtered seawater (0.8 μ Millipore filter) to which nutrients of a certain concentration were added (FCRG-Medium at half strength: *Univ. of California, Inst. Marine Resources, 1969. Research on the marine food chain; progr. rep.,*

July 1968–June 1969. Pt I. Introduction and account of work in progress, pp. 36–40. Unpubl. M. S., IMR Ref. 69–9). When fed to *Calanus helgolandicus*, these algal cultures were between 4 and 12 days old except *G. splendens* which needed longer periods to reach equivalent cell densities.

The cell diameter of *Chaetoceros curvisetus* was between 5 and 10 μ, of *Skeletonema costatum* between 5 and 8 μ, and of *Lauderia borealis* between 19 and 22 μ. The maximum width of a *Gymnodinium splendens* cell was 60 μ.

The rearing experiments were carried out in beakers and jars which had a volume of 3000 ml (nauplii), 4000 ml (nauplii and copepodites stage I) and 8000 ml (copepodites stage II to adults). To keep the algae in even suspension, a new method was used: each jar was mounted on a frame attached to an universal joint. Below frame and jar an electric motor was mounted which caused the rotation of the apparatus at a speed of 2.0 r.p.m. (Fig. 1). Samples taken from different locations in the jars showed that the algae were evenly distributed. Only *Gymnodinium splendens* aggregated to some extent close to the surface during the light period. *Calanus helgolandicus* (nauplii, copepodites and adults) moved slowly in the jars and were almost always evenly distributed. They were exposed to 12 h light and 12 h darkness.

This cultivation method exhibited several advantages for the copepods: In unagitated water where algae and fecal pellets settled fast on the bottom of the beaker the extremities (legs and antennae) of the nauplii and early copepodites were often clogged with algae or fecal material which then caused high mortalities. In the rotating cultures the extremities of any stage were never clogged. Furthermore, the setae and antennae were almost never broken or damaged. The moving water prevented the nauplii from being caught on, or attached to, the surface film of the water (CORKETT 1967). Additionally, the fecal pellets always aggregated to a heap at the center of the bottom. Therefore the animals encountered, while feeding, almost no fecal material. The slight water movement may also have helped to maintain a constantly high oxygen content in the seawater.

Measurements of the food concentration were done 1 to 4 times per day using a

Table 1

Carbon content (μg C/l) of four chain-forming diatoms and the dinoflagellate *Gymnodinium splendens*

Algae species	Carbon content (μg) of 1 mm^3 of algae volume	Number of carbon determinations	Standard deviation	Coefficient of variation
Lauderia borealis	85.0	66	± 13.8	16.2 %
Skeletonema costatum	113.2	13	± 9.2	8.2 %
Chaetoceros curvisetus	115.0	28	± 16.1	14.0 %
Gymnodinium splendens	129.2	5	± 5.3	4.1 %

Coulter Counter Model A. Measurements at different threshold settings made it possible to cover the whole size range of the algae. From the algal concentrations, expressed as μ^3 (algal volume) per liter of seawater, organic carbon concentrations per liter seawater were calculated. The organic carbon contents of the different algae were determined with a Beckman Model 15 A Infrared Analyzer (MENZEL & VACCARO 1964) after the algal volume per ml or l was measured with the Coulter Counter (Table 1). Knowing the relation of volume to carbon content for each algal species, it was possible at any time to maintain, within close limits, any desired algal carbon level.

The temperature ranged from $14.6^0 \pm 0.2^0$ C to $15.7^0 \pm 0.2^0$ C for the different jars. During the 12 h dark period each day the jars were wrapped with aluminium foil. The culture medium (seawater of 34 ‰ S), filtered through a 0.8 μ Millipore filter, was renewed every 3 to 6 days.

RESULTS

Observations started within hours after hatching and ended when 50 % of the surviving copepods had reached adulthood. Employing this 50 % value appeared to be useful because a few of the copepodites usually showed rather long delays in reaching the adult stage.

Length of the period from hatching to adulthood

Figure 2 shows the influence of food concentration and food quality on the length of the period from hatching to adulthood. Each point represents a single

Table 2

Average food concentrations in μ^3 algae/l in relation to carbon concentration (μg/l). Standard deviation and coefficient of variation are given for mm³/l

Algae species	μg C/l	10^8 μ^3 algae/l	Standard deviation	Coefficient of variation (%)
Lauderia borealis	28	3.35	± 0.47	14.0
	47	5.50	0.76	13.8
	53	6.27	1.19	19.0
	56	6.66	0.89	13.4
	116	13.76	2.45	17.8
Skeletonema costatum	52	4.58	± 0.68	14.9
	103	9.14	0.83	9.1
	106	9.32	1.09	11.7
	218	19.24	2.59	13.5
Chaetoceros curvisetus	196	17.00	± 2.08	12.2
Gymnodinium splendens	100	7.52	± 1.16	15.7

experiment starting with an average of 80 nauplii. The effect of food concentration is well demonstrated with *Calanus helgolandicus* feeding on *Skeletonema costatum* offered at concentrations between 52 μg and 800 μg organic C/l. With decreasing food concentration, the period from hatching to adulthood increases exponentially.

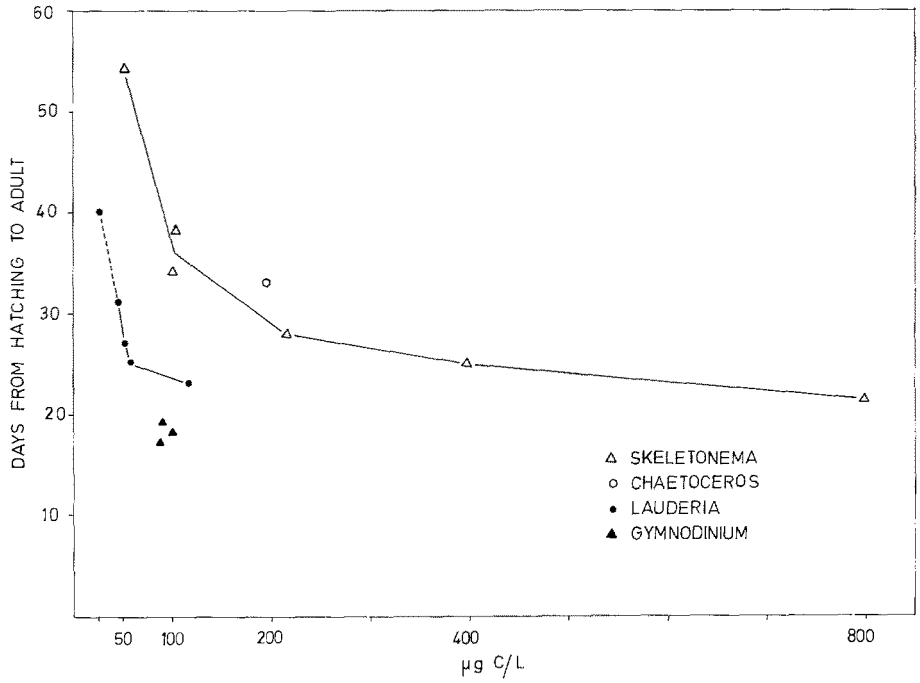

Fig. 2: *Calanus helgolandicus*. Period from hatching to adulthood as a function of food concentration and food species

In *Lauderia borealis* the results are similar. It should be noted that, due to shortage in time, the experiment at 28 μg C/l was terminated already after 2 animals had reached adulthood and 21 individuals were still copepodites of stage V.

Different food species at a concentration of 100 μg C/l, yielded different effects. With *Skeletonema costatum* as food the period from hatching to adulthood lasted 36 days; with *Lauderia borealis* 24 days; and with *Gymnodinium splendens* only 18 days. With *Chaetoceros curvisetus* only one experiment was carried out at 196 μg C/l. Table 2 shows the average food concentrations expressed in carbon units (g C/l) and volume units (μ^3/l).

Mortality

Table 3 shows the influence of different food concentrations and food quality on mortality during the entire development of *Calanus helgolandicus* from hatching to adulthood (each experiment began with an average of 80 nauplii). At 100 μg C/l,

mortality was highest (33.9 %) with *Skeletonema costatum;* it was 13.5 % with *Lauderia borealis;* and 2.3 % with *Gymnodinium splendens.* The same tendency can be seen at 50 µg C/l. Mortality clearly increases with decreasing food concentration.

Table 3

Influence of food concentration and food species on mortality rates (%) of *Calanus helgolandicus*

Food concentration	*Skeletonema costatum*	*Lauderia borealis*	*Gymnodinium splendens*
200 µg C/l	26.2 %	—	—
100 µg C/l	33.9 %	13.5 %	2.3 %
50 µg C/l	41.3 %	33.5 %	—
28 µg C/l	—	58.2 %	—

As mentioned earlier, the experiment at 28 µg C/l with *Lauderia borealis* could not be finished; however, this has no influence on the mortality data (100 µg < 50 µg < 28 µg C/l) because the value of 58.2 % (Table 3) can only increase.

When raising *Rhincalanus nasutus* and *Calanus helgolandicus* from egg to adulthood, MULLIN & BROOKS (1968) showed that mortality was highest during the early stages (nauplii, copepodite stages I and II). Figure 3 illustrates the survival

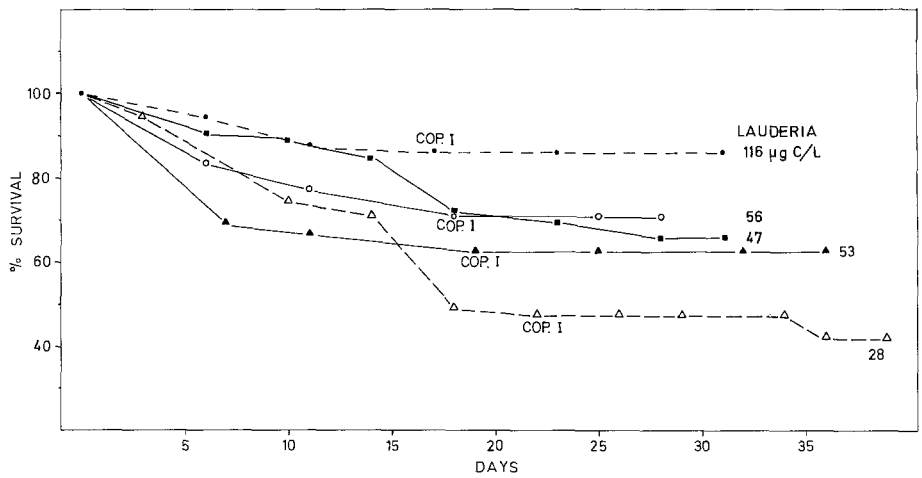

Fig. 3: Survival rates of *Calanus helgolandicus* during its entire development as a function of food concentration (food source: *Lauderia borealis*)

of *Calanus helgolandicus* (continuous cultures) during the entire development at different food concentrations of *Lauderia borealis.* At 53 µg, 56 µg and 116 µg C/l there was no mortality after copepodite stage I; at 28 µg and 47 µg C/l a few individuals died. Figure 3 demonstrates that mortality is highest during the early

stages up to copepodite stage I. This is true not only with *Lauderia borealis* as food but also with *Gymnodinium splendens* and *Skeletonema costatum.*

Size of adult females

To determine whether food concentration and food quality have an effect on the size of the copepods, 10 to 41 females from each experiment were killed in 2 % formalin upon reaching the adult stage. Immediately afterwards their total length was measured using a binocular microscope. Figure 4 presents the results of these measurements. There appears to be a strong relationship between the different food concentrations *(Lauderia borealis* and *Skeletonema costatum)* and the length of the females: with increasing food concentration *(Skeletonema costatum)* the length of the females approaches a maximum value asymptotically. The same tendency applies

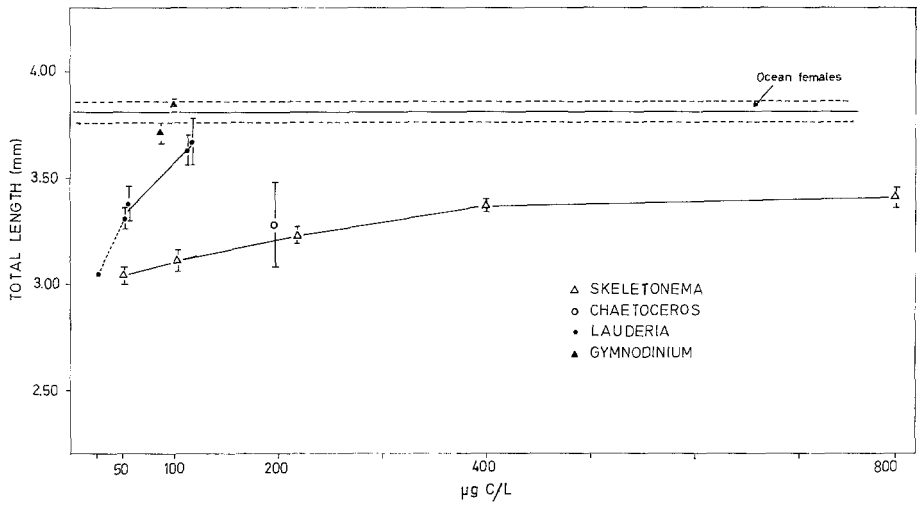

Fig. 4: Total length of *Calanus helgolandicus* females as a function of food concentration and food quality. (The marks are 95 % confidence limits)

with *Lauderia borealis* as food although the point obtained at 28 µg C/l, as previously mentioned, consists only of measurements on 2 females. Thus, the 4 algal species used as food had an entirely different effect on the body length of female *Calanus helgolandicus.* While the *S. costatum*-fed females attained, at approximately 100 µg C/l, an average length of 3.11 mm, the *L. borealis*-fed females reached a length of 3.65 mm and those fed *G. splendens* 3.71 and 3.84 mm, respectively.

In order to allow comparison with these laboratory data, the lengths of females caught in the ocean during June and July 1969 have also been plotted in Figure 4. Their average length is 3.81 mm which is close to the *G. splendens* and *L. borealis* values at 100 µg C/l.

Sex ratio

Table 4 shows that the 4 algae used as food exert a different effect on the sex ratio of *Calanus helgolandicus*. With *Chaetoceros curvisetus* no males appeared; with *Skeletonema costatum* the percentage of males was very low (although survival rates were high); with *Gymnodinium splendens* the percentages of males were 22.7 % and 24.4 %, respectively (mortality 2.3 %).

Table 4

Sex ratio of *Calanus helgolandicus* (% males) fed different algae species at different concentrations

Algae species	Food concentration (μg C/l)	Males (%)	Mortality (%)
Chaetoceros curvisetus	196	0	47
Skeletonema costatum	100	1.6	33.9
	218	1.4	26.2
Lauderia borealis	116	4.7	13.5
unagitated	approx. 400	20.0	approx. 40
unagitated	approx. 400	24.4	approx. 40
Gymnodinium splendens	100	24.4	2.3
	100	22.7	2.3

Another experiment with 356 nauplii yielded 301 females and 7 males (mortality 13.5 %) with a mixture of *Chaetoceros curvisetus* and *Skeletonema costatum* (both algae together represented a concentration of approximately 600 μg C/l).

All these results lead to the assumption that different food species cause different sex ratios and that food quality may be one of the major factors influencing sex ratio. This assumption requires verification; it is possible for example that the individuals which died would have become males, i. e., that selective mortality may have influenced the results presented here.

Fecundity and hatching rate

Additional experiments were undertaken to find out whether fertilization occurs under laboratory conditions. Between 5 and 15 males and 5 to 19 copepodites stage V were placed in a modified "planktonkreisel" (GREVE 1968) filled with 20 liters of seawater. *Lauderia borealis* and *Gymnodinium splendens* were offered as food. In 4 cases fertilization was observed. Only 3 of the 4 females could be used for fecundity experiments because the fourth female had not been kept under controlled conditions. Five spermatophore-carrying females from the ocean and these three laboratory grown and fertilized females were each placed in 800 ml seawater (1000 ml-beaker) and fed *Lauderia borealis* at a concentration of approximately 400 μg C/l.

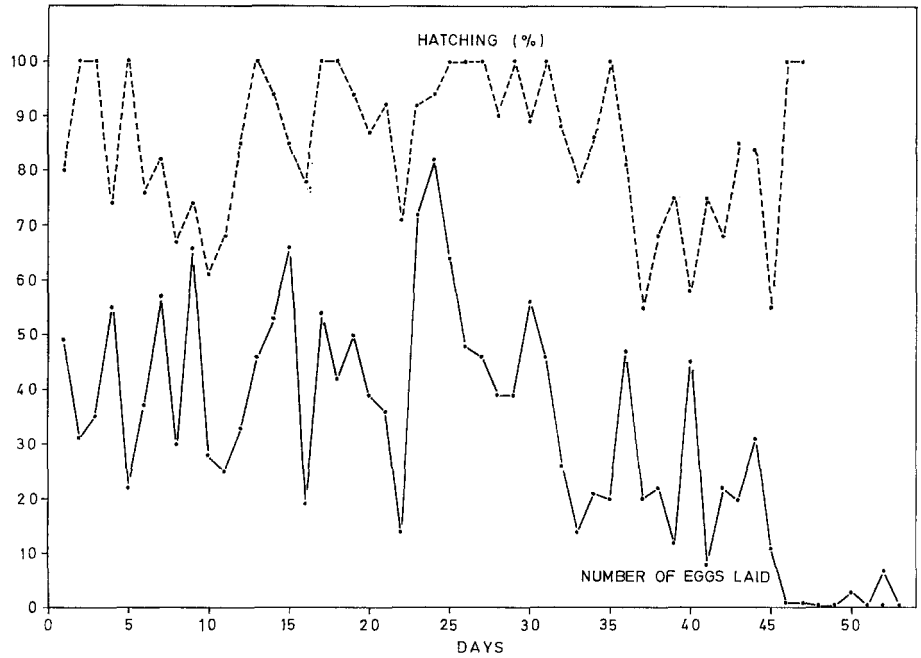

Fig. 5: Fecundity and hatching percentage of a laboratory-raised and fertilized *Calanus helgolandicus* female from day of fertilization

All females began to lay eggs 1 to 2 days after fertilization. Egg laying continued throughout the observation period (Fig. 5). Each beaker was checked every day to pick out the fertilized eggs deposited during the last 24 h. In most cases the eggs were laid in clusters on the beaker bottom; these clusters appeared not to be eaten by the females.

Table 5 reveals that the average number of eggs fertilized under laboratory conditions is close to the average number per female in the ocean. The percentage of successful hatchings was slightly higher in laboratory spermatophored than in ocean spermatophored females.

Table 5

Fecundity and hatching percentage of *Calanus helgolandicus* females

Kind of females	Number of females	Average number of fertilized eggs	Number of eggs laid minimum	maximum	Hatching percentage
Females raised and fertilized under laboratory conditions	3	1991	1704	2080	84 % (79 %—87 %)
Spermatophore carrying females from the ocean	5	2267	1233	3188	77 %

It appears that there is no striking difference in fecundity and hatching percentage between females cultivated in the laboratory and those in the ocean. Among the second generations produced by laboratory spermatophored females were many males. Unfortunately, these males were apparently unable to copulate and, therefore, no third generation was obtained. From many observations it appears that the condition of the males largely determines whether copulation occurs or not. It may be interesting in this connection to note that males which originated from *Gymnodinium splendens*-fed cultures were more active and more difficult to catch than those which originated from *Skeletonema*-fed cultures.

DISCUSSION

In order to critically assess our results we must take into account some parameters which strongly influence the life of *Calanus helgolandicus*. Among these are the food species and food concentrations encountered. The Food Chain Research Group of the University of California, Institute of Marine Resources, La Jolla, determined from April 26, 1967 to September 13, 1967 the concentration of living phytoplankton and the numerical abundance of many phytoplankton species in the Pacific Ocean off La Jolla (RESEARCH 1968). From these data MULLIN & BROOKS (1969) estimated that the average phytoplankton concentration off La Jolla ranges throughout the year from 10 μg to 50 μg C/l with peaks near 300 μg C/l. Most of the results presented in this paper are based on experiments carried out at food concentrations close to those in the ocean (28 μg to 116 μg C/l). NICHOLLS (1933) found that *Calanus finmarchicus* needs 28 days to reach adulthood when kept at 14° to 15° C. MULLIN & BROOKS (1967) suggested from field observations that *C. helgolandicus* has a generation time of approximately 4 weeks. Looking at the results presented in Figure 2, the period of 4 weeks corresponds to a food concentration of 210 μg C/l *(Skeletonema costatum)* or 50 μg C/l *(Lauderia borealis)*. The *Lauderia borealis* concentration is very close to natural conditions and leads to the following assumption: although the smaller algal species, *Chaetoceros curvisetus* and *Skeletonema costatum*, are far more abundant than large species of the genera *Coscinodiscus, Stephanopyxis* and *Lauderia* in ocean waters off La Jolla, *Calanus helgolandicus* selects preferably the larger cells (RICHMAN & ROGERS 1969) and, therefore, keeps the concentrations of larger algae down. By ingesting larger cells or cell chains, *C. helgolandicus* obtains more food than by eating smaller algae like *C. curvisetus*.

MULLIN & BROOKS (1968) carried out growth and rearing experiments with the marine copepod *Rhincalanus nasutus*. Feeding the diatom *Ditylum brightwellii* at an average concentration of 148 μg C/l resulted in 23 % mortality during the period from hatching to adulthood, whereas feeding *Thalassiosira fluviatilis* at 196 μg C/l led to a mortality of 56 %.

According to Figure 4, only *Calanus helgolandicus* females fed *Lauderia borealis* and *Gymnodinium splendens*, at concentrations of 100 μg C/l, reach the same size as females from the ocean. Females kept at 50 μg C/l *(L. borealis)* remain significantly smaller than ocean females (the average food concentration in the ocean generally

did not exceed 50 µg C/l). STRICKLAND (1968) presented chlorophyll measurements in the Pacific Ocean using an in vivo fluorometer. He detected thin layers (2 to 3 m thickness) of high chlorophyll content (up to 10 µg/l) which were surrounded by

Table 6

Feeding of *Calanus helgolandicus* copepodites stage V on three phytoplankton species (food concentration 100 µg C/l)

Algae species	Algae ingested per individual per h (mm^3)	Ingested per individual per h (µg C)	Number of individuals (Cop. St. V) in 7000 ml
Skeletonema costatum	0.035 (0.021—0.060)	4.0	35 to 68
Lauderia borealis	0.131 (0.086—0.157)	11.1	47 to 63
Gymnodinium splendens	0.105 (0.082—0.125)	13.6	31 to 44

water masses with a far lower chlorophyll content. This finding proves again that phytoplankton is often distributed in layers or patches. It seems that *Calanus helgolandicus* which reach adulthood in the sea have spent most of their life in such dense layers or patches; it appears impossible that in the ocean females attain their rather large size at food concentrations of 10 µg to 50 µg C/l. In the dense phytoplankton layers, however, concentrations of 100 µg C/l or more are frequently encountered.

Up to now few studies have been carried out on the fecundity of calanoid copepods. MARSHALL & ORR (1952) found a maximum egg production in *Calanus finmarchicus* of 586 eggs per female. MULLIN & BROOKS (1967) fed *C. helgolandicus* and *Rhincalanus nasutus* females the diatoms *Thalassiosira fluviatilis* and *Ditylum brightwellii; Calanus helgolandicus* females laid 613 or 691 eggs per female, *R. nasutus* up to 355 eggs. CONOVER (1967) investigated the egg production of the cold water species *Calanus hyperboreus* and found an average of 1340 eggs per female (maximum of 3800 eggs). MARSHALL & ORR (1952) reported that *Calanus finmarchicus* females lay different amounts of eggs when fed different phytoplankton forms. The largest number of eggs was laid by females offered *Lauderia sp.*

The average number of eggs laid by *Calanus helgolandicus* in our experiments were 1991 per laboratory female and 2267 eggs per ocean female. These are the highest egg numbers, produced by calanoid copepod females.

Figures 2 and 4 as well as Table 3 show that, at the same food concentration (100 µg C/l), different algae food may cause differences in (a) length of the period from hatching to adulthood, (b) mortality and (c) size of females. Does food quality or food quantity (amount of food ingested) cause these differences? Table 6 presents data on the feeding of *Calanus helgolandicus* copepodites (stage V) on *Skeletonema costatum, Lauderia borealis* and *Gymnodinium splendens* at concentrations of 100 µg C/l. The volume of food ingested per individual decreases in the order *L. borealis, G. splendens, S. costatum*; the amount of carbon ingested per individual in the order *G.*

splendens, L. borealis, S. costatum. The carbon data seem more relevant since the amount of carbon per algae cell gives a better estimate of the plasma volume, and therefore, of the food amount consumed, than cell volume (STRATHMANN 1967). The carbon amounts of *G. splendens* ingested are 3.4 times higher than those of *S. costatum*; the amounts of *L. borealis* 2.8 times higher than those of *S. costatum.* These data lead to the assumption that the different amounts of food (carbon) ingested cause the differences mentioned above (not the different food qualities).

According to ADAMS & STEELE (1966) *Calanus* stops feeding at a particulate organic carbon concentration of approximately 70 μg C/l. PARSONS et al. (1969) found that *Calanus plumchrus, Calanus pacificus* and *Pseudocalanus minutus* cease to feed at minimum phytoplankton concentrations between 50 μg and 190 μg C/l. In our experiments, *Calanus helgolandicus* copepodites graze both *Lauderia borealis* and *Gymnodinium splendens* down to 15–20 μg C/l, and *Skeletonema costatum* down to 30 μg C/l. Several explanations can be offered to account for these differences:

(1) The size of the food organism can affect the level at which feeding ceases.

(2) Different culture methods may yield different results. ADAMS & STEELE (1967) used for their grazing experiments container sizes ranging from 180 ml to 1000 ml. PARSONS et al. (1969) chose for their grazing experiments bottle sizes of 1000 ml. During our investigations jars were used which contained 7000 ml of seawater. It is assumed that beaker size influences the feeding behaviour and therefore the feeding intensity of planktonic copepods. In addition, in our experiments the algae were evenly distributed in the 7000 ml of seawater.

(3) The physiological condition of copepods taken from the sea may vary to a large extent. In our experiments, all individuals were reared under controlled conditions; almost all copepods were active and their antennae and setae undamaged.

(4) Adaptation to certain food concentrations previous to the grazing experiment may cause a feeding to cease at lower or higher food concentrations. The copepodites which grazed *Lauderia borealis* and *Gymnodinium splendens* down to 15–20 μg C/l were kept throughout their life at average food concentrations of 50 μg and 100 μg C/l, respectively; these algal concentrations are frequently encountered in the Pacific Ocean off La Jolla.

From all data available it can be concluded that *Calanus helgolandicus* does not require a combination of several algal species to reach adulthood, but is able to develop from hatching to adulthood with low mortality rates when fed at natural concentrations exclusively on *Chaetoceros curvisetus* or *Skeletonema costatum* or *Lauderia borealis* or *Gymnodinium splendens.*

The factors which cause a 50 : 50 sex ratio remain unclear. I intend to pay special attention to the problem of environmental control of the sex ratio in *Calanus helgolandicus* in the near future.

SUMMARY

1. *Calanus helgolandicus* was grown from egg to adult in agitated seawater cultures at 15° C in the laboratory.

2. The chain-forming diatoms *Chaetoceros curvisetus, Skeletonema costatum, Lauderia borealis* and the dinoflagellate *Gymnodinium splendens* were offered as food. The concentration of food, resembling phytoplankton concentrations found in the ocean off La Jolla, ranged from 28 μg to 800 μg carbon per liter.
3. Depending on food quality and food concentration, the time from hatching to adulthood lasts between 18 and 54 days. Mortality from hatching to adulthood ranges from 2.3 % to 58.2 %. The length of adult females is directly related to the amount of food offered; it ranges from 3.03 mm to 3.84 mm.
4. The sex ratio in different batches of laboratory grown copepods varies considerably. The largest percentage of males (about 25 %) was obtained with *Lauderia borealis* or *Gymnodinium splendens* as food source.
5. The fecundity of females grown and fertilized under laboratory conditions averages 1991 eggs per female with a hatching percentage of 84 %. These values are close to those obtained from spermatophore-carrying females from the ocean (2267 eggs per female; hatching percentage 77 %).

Acknowledgements. This research was supported in full by the United States Atomic Energy Commission, Contract No. AT (11–1) GEN 10, P.A. 20. I am indebted to Miss Y. PINCHANSKI, Mrs. J. E. PRESLAN, Miss G. K. PREVOST, Mr. J. B. JORDAN and Mr. R. J. LINN for extensive and valuable assistance; I also wish to thank Dr. J. BEERS for critically going through the manuscript and Dr. J. D. H. STRICKLAND for generous support and helpful suggestions throughout the course of this work.

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