

Food regulation of growth and maturation in a natural population of *Aurelia aurita* (L.)

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Abstract. Growth and maturity development of the moon jellyfish, *Aurelia aurita*, were recorded in Vågsbøpollen, a small and semi-enclosed bay on the Norwegian west coast, and compared to those of medusae transferred to excess food and starving conditions, respectively. Mesozooplankton were extremely scarce in Vågsbøpollen. The abundance and biomass of the medusae in the poll were higher than those typically found in open waters, reaching a maximum of 22 ind. m⁻³ and 710 mg C m⁻³ in June. The average diameter of medusae in the poll increased to 8 cm until the last part of June, with an instantaneous growth rate between 1.5 and 20% day⁻¹, thereafter retarding somewhat, giving a negative growth rate of up to 2.6% day⁻¹. Starving medusae showed a negative growth rate of up to 13.4% day⁻¹, and all the medusae were dead after 49 days. Well-fed medusae showed a very stable growth over a 56 day period, diverging from the poll population from early June, and with a growth rate between 3.8 and 9.8% day⁻¹. Medusae from the poll population began carrying planulae on their oral arms when at least 5 cm in diameter, whereas not even the largest medusa of 15.6 cm diameter among those in the well-fed group produced any planulae. For the first time, it is thus explicitly shown that the size and maturity of *A. aurita* are externally controlled through food availability. Scarcity of food reduces the growth rate, but also changes the energy allocation towards reproduction, which thus occurs at a smaller size than for well-fed medusae. Its plasticity makes it possible for this species to exploit environments with low advection of food and develop high abundance in such environments, without losing fecundity.

Introduction

The moon jellyfish, *Aurelia aurita*, is a cosmopolitan species found in the waters of Japan (Yasuda, 1971; Ishii *et al.*, 1995; Omori *et al.*, 1995), as well as in the coastal waters of Europe (Möller, 1980; Hernroth and Gröndahl, 1985; van der Veer and Oorthuysen, 1985; Schneider, 1989; Lucas and Williams, 1994; Olesen *et al.*, 1994; Schneider and Behrends, 1994; Lucas, 1996) and North America (Hamner and Jenssen, 1974). The pattern of the population dynamics varies, with the maximum abundance usually being <1 individual (ind.) m⁻³ in open coastal waters (cf. Möller, 1980). Reports from two enclosed areas have indicated considerably higher abundance, with up to 25 ind. m⁻³ (Lucas, 1996) and 300 ind. m⁻³ (Olesen *et al.*, 1994), but the maximum average diameter only reached 5.4 and 3.7 cm, respectively, in these environments, whereas the maximum average diameter reported for more open areas ranges from 20 to 30 cm (cf. Möller, 1980; Schneider and Behrends, 1994). These findings indicate that food shortage restricted growth in the densely populated environments, and it has been assumed that there is a density-dependent regulation mechanism for *A. aurita* populations (Schneider and Behrends, 1994). However, although it is a logical suggestion to explain the small size as an effect of food shortage, it has not

hitherto been specifically shown that food regulates the individual growth within such populations. Furthermore, because reproduction, as reported for more open environments, occurs when the medusa has reached at least 7–8.5 cm diameter (Yasuda, 1971; Omori *et al.*, 1995), the consequences of the small size in enclosed areas may also include a dramatic reduction in reproductive output, if size at maturity is the same as that in the open environments.

Vågsbøpollen is a semi-enclosed bay with an annual population of *A. aurita* that occurs in much higher abundance than in the nearby open water (Berstad *et al.*, 1995). This environment is connected to open water through a very shallow channel of ~600 m length, leading to Kviturdvickpollen, which in turn is connected to a deeper channel of ~600 m length, leading to more open water (Figure 1). Although tidal currents cause some renewal of the water (cf. Dybern, 1967), exchange of medusae between the inner and outer populations is probably very limited, due to the length and shallowness of the entrance system. This locality is, therefore, ideal as a study site for the growth and development of *A. aurita*. Furthermore, because the density-dependent growth hypothesis (cf. Schneider and Behrends, 1994) has not been evaluated experimentally, a simple design where the natural population is compared with well-fed animals would give us the opportunity to do so. In this paper, we therefore report the results from an investigation where the growth and development of medusae in Vågsbøpollen were compared to those of poll medusae transferred either to conditions of excess food or to starving conditions.

Method

Aurelia aurita was sampled between 29 April and 16 July 1996 in Vågsbøpollen, south of Bergen, Norway (Figure 1), and all experiments were performed at the marine biological station of the University of Bergen, situated close to the study locality. Vågsbøpollen is a semi-enclosed bay with a maximum length/width of 1300/300 m, and a maximum depth of 12 m (Dybern, 1967). Sampling of *A. aurita* was conducted weekly in the deepest part by using a 500 µm mesh dip net, with a 10 l plastic bag as non-filtering cod end. The net was towed for 5 min in the surface water at a constant speed. Surface water temperature was measured simultaneously. Once a month, zooplankton were sampled with a vertical haul, using a 180 µm meshed conical net, and the sample was immediately preserved in 5% formalin for later microscopic analysis at the laboratory. Collected medusae were kept in carboys of ~30 l volume, filled with local surface water during transportation to the laboratory. After returning to the laboratory, less than 1 h after sampling, the diameter of each individual was measured to the nearest millimeter using a Wild M5 dissection microscope (small medusae) or directly by eye, using a millimeter graded ruler, and the presence of eggs and planula larvae of *A. aurita* was recorded. Measurements were made by placing an individual medusa with exumbrella down in a large Petri dish with sea water, avoiding exposure in the air as far as possible. The abundance of *A. aurita* was calculated from the number of sampled medusae by assuming a filtering efficiency of 100% for the full 5 min tow, giving the volume filtered as net-opening area times towed distance.

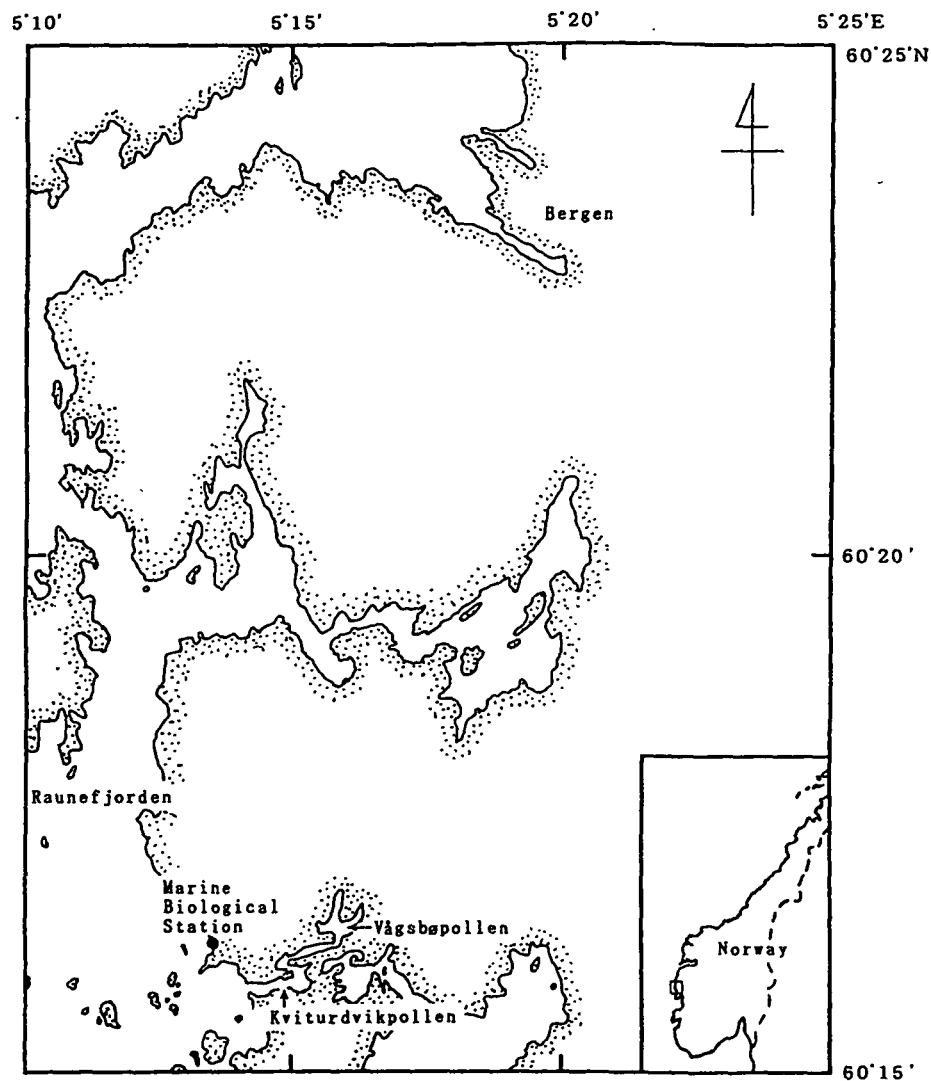


Fig. 1. Sampling area of *A. aurita* in Vågsbøpollen, south of Bergen.

The hydrographic conditions, including salinity, were similar to those for medusae used by Båmstedt (1990), so the dry weight (DW; mg) of individual *A. aurita* medusae was estimated from the equation of Båmstedt (1990):

$$DW = 0.002 \times D^{2.899}$$

where D is the diameter in millimeters. The dry weight was converted to carbon assuming 4.3% of dry weight (Larson, 1986). The instantaneous growth rate (μ ; day⁻¹) was calculated on the basis of increments in dry weight:

$$\mu = \ln(W_2/W_1)/(t_2 - t_1)$$

where W_1 and W_2 are the dry weights, and t_1 and t_2 are the day numbers on two consecutive analyses.

Aurelia aurita for tank experiments were sampled in Vågsbøpollen on 22 May 1996 in the same way as in the population study. After returning to the laboratory, the collected medusae were transferred to outdoor cylindrical tanks of 200 l volume, filled with continuously aerated sea water. The tanks were placed within bigger tanks with flow-through sea water, in order to maintain a constant temperature, and the whole construction was covered with a roof, eliminating direct sunlight. Seven tanks were used, each of them loaded with 8–13 individuals randomly selected from the stock of collected medusae. Five of the tanks were given food in excess in order to saturate feeding of the medusae, and the remaining two tanks were kept without any food. Zooplankton as food were collected by a 300 µm meshed net from Raunefjorden close to the laboratory, and consisted of ~90% in volume of copepodids of *Calanus finmarchicus* and the lobate ctenophore *Bolinopsis infundibulum*. The bell diameter and the presence of eggs and planula larvae of *A. aurita* were analyzed weekly in the same way as for the field medusae, and both the water and the food renewed.

The sex of immature individuals was indistinguishable in the dissection microscope. Medusae were therefore classified as follows: (1) males and unripe females with no visible gametes in gonads; (2) unripe females, but their oocytes visible in gonads; (3) ripe females with mature oocytes in gonads, and fertilized eggs and planula larvae in brood sacs on oral arms; (4) ripe females with fertilized eggs and planula larvae in brood sacs on oral arms, but no visible oocytes in gonads.

Results

Zooplankton sampled with a 180 µm meshed net were extremely scarce in the monthly samples, with a maximum abundance of 6.2 ind. m⁻³, and consisted mainly of the two hydromedusae *Clytia quadrata* and *C. hemisphaerica*.

Aurelia aurita were present in Vågsbøpollen throughout the sampling period and Figure 2 illustrates its average abundance, biomass and instantaneous growth rate during the period. The temperature rose gradually from April to June (8–15°C), climbing up to a maximum on 9 July (15.8°C), and with a slight decrease to 13.5°C on 16 July (Figure 2). The abundance of medusae was high throughout the period, with the highest values at the start (16 ind. m⁻³ in late April) and in June (4–22 ind. m⁻³), and with no significant temporal trend. The biomass was low in April and May, but steadily rising from ~4 mg C m⁻³ on 29 April to ~20 mg C m⁻³ on 13 May. Peak biomass for the period was recorded on 24 June, at ~710 mg C m⁻³, after which the biomass decreased to ~100 mg C m⁻³ when the study ended on 16 July. The average instantaneous growth rate varied considerably, but showed a clear decreasing temporal trend, with a peak value on 10 May of 0.25 day⁻¹, and close to zero during the summer.

The individual size ranged from 0.2 to 2.9 cm diameter on 29 April, with the peak in the size class 1.0–2.0 cm diameter, indicating a recruitment mainly before

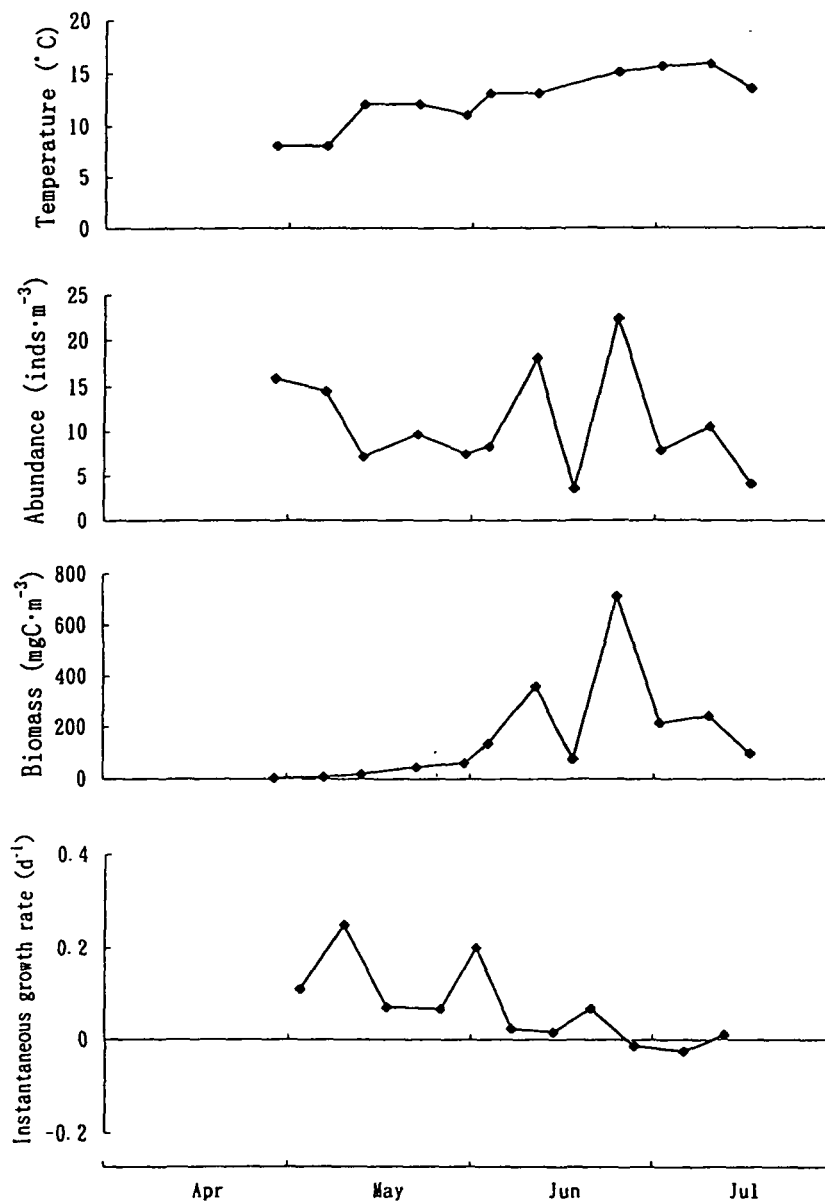


Fig. 2. Water temperature and abundance, biomass and instantaneous growth rate of *A. aurita* in Vågsbøpollen.

29 April (Figure 3). The two smallest size classes gradually disappeared, indicating that strobilation was not continuous. An approximately normal distribution was sustained throughout the investigation, confirming the homogeneity of the population, with no recruitment or mixing with other populations. However,

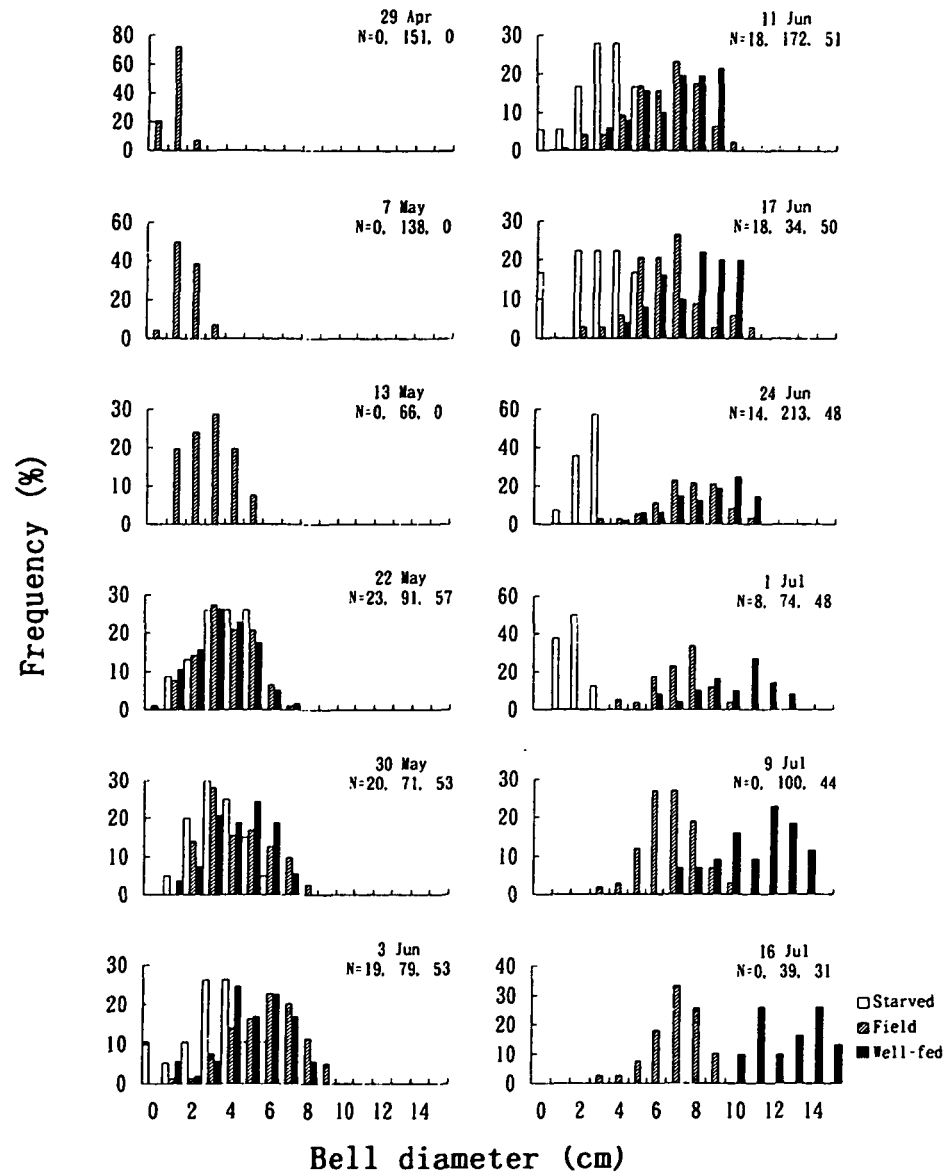


Fig. 3. Percentage frequency distributions of the bell diameter of *A. aurita* in Vågsbøpollen and of starved and well-fed ones cultured in the tank. N is the number of starved individuals, those collected in the field, and well-fed ones, from left to right, respectively. The culture experiments were started on 22 May and all starved individuals were dead after 1 July. The data of starved ones on 28 June were not included.

median and mean size only increased until 24 June, when the largest medusa size of 11.8 cm was observed, thereafter retarding somewhat through a decreased frequency of the largest medusae.

The size frequency of *A. aurita* kept in tanks with excess food was similar to the field sampled population during the three first sampling occasions, but diverged thereafter, through a higher increase in large medusae and a continuous gradual increase in the size distribution throughout the study (Figure 3). The size frequency of *A. aurita* kept in starving conditions diverged rapidly from the well-fed group (Figure 3), and all the medusae were shrunk and dead after 1 July.

The mean bell diameters of medusae from the two experimental groups and from the field population are displayed in Figure 4. All three groups showed identical initial values at the start, 22 May, but starving animals reduced size steadily, showing an average diameter of 2.3 cm after 6 weeks, and were all dead on 9 July. The average size of the two other groups began to diverge in June and this difference was exaggerated after 24 June. Well-fed medusae showed a linearly increased trend in bell diameter, whereas the field medusae stopped growth completely. A summary of the average instantaneous growth rate of the three groups at different periods is displayed in Table I.

The relative proportions of females in different maturity stages are given for the natural field population (Figure 5A) and the experimental well-fed group (Figure 5B). In the natural population, sexually immature females dominated until the end of May, when the population was composed of metephyrae and small medusae. The percentage of sexually mature females increased during June and July as gonad development progressed. Females with the oocytes in gonads were first found on 11 June and the percentage increased to 39.9% on 24 June, thereafter decreasing gradually. Ripe females with planulae were first observed on 17 June and this stage increased to 43.6% on 16 July. On 9 July, females with empty gonads and planulae on the oral arms were first observed, and their percentage increased to 7.7% on 16 July. The minimum bell diameter of females with oocytes in gonads and with both eggs and planulae was 5.0 cm.

In the experimental well-fed group, females with the oocytes in gonads were first identified on 24 June, and the percentage increased to 61.3% on 16 July

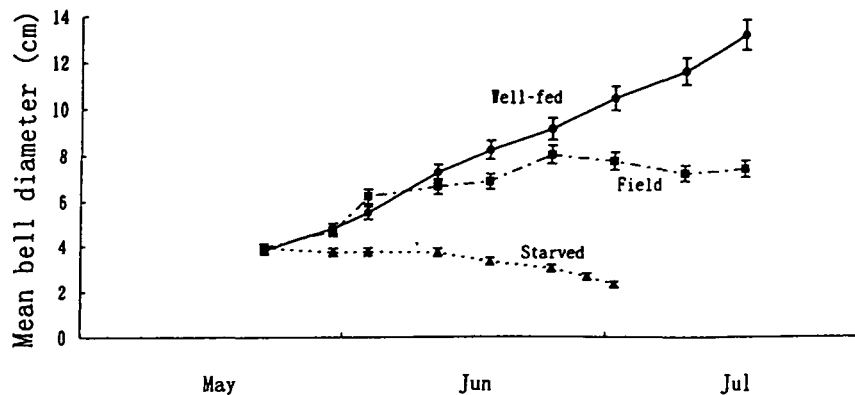
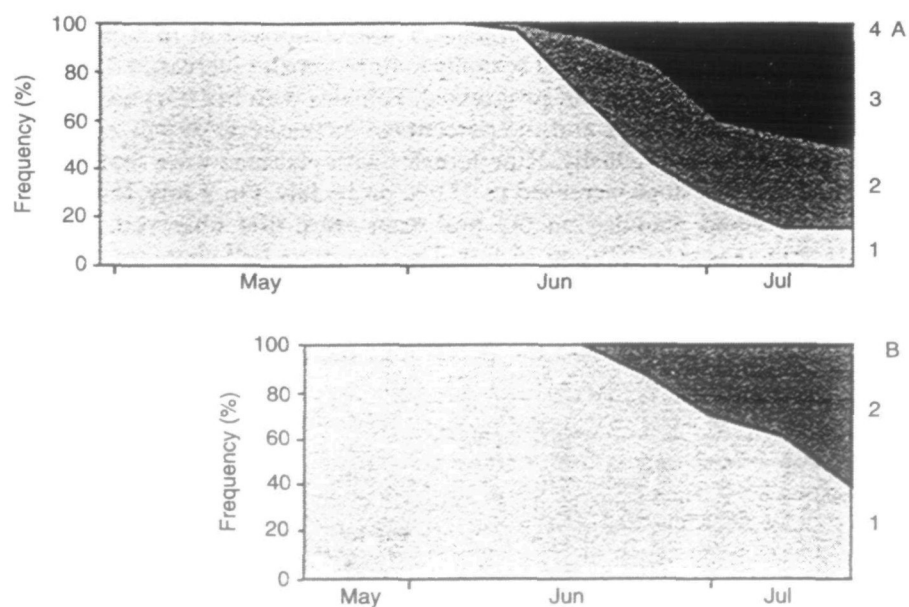


Fig. 4. Mean bell diameter of *A. aurita* in Vågsbøpollen and of well-fed and starved individuals cultured in the tank.

Table L. *Aurelia aurita*: instantaneous growth rate within each period in the field and cultured individuals in the tank

Period	Instantaneous growth rate (day ⁻¹)		
	Field	Tank	
		Starved	Well-fed
22–30 May	0.065	–0.020	0.085
30 May–3 June	0.202	0.002	0.097
3–11 June	0.023	–0.003	0.098
11–17 June	0.015	–0.054	0.062
17–24 June	0.066	–0.040	0.042
24–28 June	–	–0.091	–
28 June–1 July	–	–0.134	–
24 June–1 July	–0.014	–	0.055
1–9 July	–0.026	–	0.038
9–16 July	0.011	–	0.052

**Fig. 5.** The percentage ratio of (1) males and unripe females with no visible gametes in gonads, (2) unripe females, but their oocytes visible in gonads, (3) ripe females with mature oocytes in gonads, and fertilized eggs and planula larvae in brood sacs on oral arms, (4) ripe females with fertilized eggs and planula larvae in brood sacs on oral arms, but no visible oocytes in gonads, to all *A. aurita*, in Vågsbøpollen (A) or in the tank with well-fed individuals (B).

(Figure 5B). No *A. aurita* with planula larvae were observed in the study period. The minimum bell diameter of medusae with oocytes in the gonads was 9.4 cm. Not even the largest females with a bell diameter of 15.6 cm had developed

planula larvae. In the experimental starved group, no *A. aurita* with the oocytes in gonads or planulae were observed.

If we assume that all medusae in category 1 (Figure 5) from 16 July were males, the proportion of males in the field population was only 15.4% and that in the well-fed experimental group was 38.7%, although the latter might be an over-estimation, because there was no sign of leveling off at this level.

Discussion

The tidal effect of the water changes in Vågsbøpollen is restricted through the narrow channel between Vågsbøpollen and the nearby Kviturdvikkollen, thereby probably making the internal production of zooplankton the main source of food for *A. aurita*. The biomass of zooplankton such as copepods was very low throughout the investigation, so *A. aurita* was apparently under food-limited conditions, although zooplankton not retained by the 180 µm meshed net might have been available. However, the most characteristic feature of the population was the high abundance, small average size and size at maturity, all indicating food scarcity. A survey of the literature data shows a large variability in population characteristics (Yasuda, 1971; Hamner and Jenssen, 1974; Möller, 1980; Hernroth and Gröndahl, 1985; van der Veer and Oorthuysen, 1985; Schneider, 1989; Lucas and Williams, 1994; Olesen *et al.*, 1994; Schneider and Behrends, 1994; Ishii *et al.*, 1995; Omori *et al.*, 1995; Lucas, 1996). We have compiled such data, especially related to how open the environments occur, i.e. open, semi-enclosed and enclosed areas (Table II). The locality and the pattern of population dynamics of *A. aurita* in this study were similar to those from Kertinge Nor in Denmark (Olesen *et al.*, 1994) and the enclosed, man-made Horsea Lake in England (Lucas, 1996). The abundance of *A. aurita* in Vågsbøpollen was considerably higher than that in most open-water areas, but lower than that in Kertinge Nor and Horsea Lake (Table II). The semi-enclosed and enclosed environments diverge from the open environments by showing a range in abundance of 9–300 medusae m⁻³ compared to 0.01–1.5 medusae m⁻³ in the open environments. Accordingly, peak bell diameter reported from open waters showed a range from 20 to 30 cm, whereas medusae from semi-enclosed/enclosed areas reached a peak diameter of 4–10 cm, and the maximum observed diameter showed the same trend. The few data available on minimum size at maturity (Table II) do not contradict the hypothesis of smaller size in non-open environments.

Schneider and Behrends (1994) suggested that the years of small-sized *A. aurita* of high abundance and the years of large-sized individuals of low abundance indicate the regulation mechanism of their density by food availability. In Vågsbøpollen, food was apparently restricted to small hydromedusae and potentially also to microzooplankton, although prey in the size range of ciliates and rotifers do not seem to contribute substantially to the energy budget of *A. aurita* (Båmstedt, 1990). The situation is thus similar to other non-open areas, where food limitation is suggested as the explanation for the poor growth of medusae (Olesen *et al.*, 1994; Lucas, 1996). Through our experimental approach, we have proved for the first time that food availability is really a controlling factor for the

Table II. *Aurelia aurita*: review of the population studies

Area index	Location	Abundance (ind. m ⁻³)	Max bell diameter (cm)	Max mean bell diameter (cm)	Min bell diameter at maturity (cm)	References
o	Tokyo Bay, Japan	nd	nd	23	nd	Ishii <i>et al.</i> (1995)
o	Tokyo Bay, Japan	1.53	31	nd	8.5	Omori <i>et al.</i> (1995)
o	Kiel Bight, western Baltic	0.16	30–33	22.5	nd	Schneider and Behrendts (1994) ^a
o	Kiel Bight, western Baltic	0.006	39–42	30.3	nd	Schneider and Behrendts (1994) ^b
o	Kiel Bight, western Baltic	0.23	nd	22	nd	Schneider (1989) ^c
o	Kiel Bight, western Baltic	0.04	nd	30	nd	Schneider (1989) ^d
o	Wadden Sea, Netherlands	0.25	nd	24	nd	van der Veer and Oorhuysen (1985) ^e
o	Wadden Sea, Netherlands	0.49	nd	20	nd	van der Veer and Oorhuysen (1985) ^f
o	Kiel Bight, western Baltic	0.33	44	19.7	nd	Möller (1980)
o	Urazoko Bay, Japan Sea	nd	31	22	7	Yasuda (1971)
s	Southampton Water, England	8.71	15	10	6.4	Lucas and Williams (1994)
s	Kertinge Nor, Denmark	300	nd	3.7	nd	Olesen <i>et al.</i> (1994)
s	Vågsbøpollen, Norway	22.3	11.8	8	5	Present study
e	Horsea Lake, England	24.9	10.5	5.38	1.9	Lucas (1996)

Area index: o, open water; s, semi-enclosed water; e, enclosed water; nd, no data.

^aData of 1982.^bData of 1984.^cData of 1982.^dData of 1983 and 1984.^eData of 1981.^fData of 1982.

growth of medusae in natural environments. The experiments also proved that the maturation process is strongly governed by food availability, and the experimental observations were thus in line with the field observations reported in the literature (see Table II), where open waters show larger size at maturity than semi-enclosed and enclosed areas. The same observations have been made from Ninegret Pond, Charlestown, Rhode Island, where growth and size at maturity are considerably lower in the semi-enclosed saltwater pond than outside in the Block Island Sound (B.Sullivan, personal communication). Thus, food availability seems to give a general explanation for both individual growth of the medusa and its maturation, but it cannot explain why semi-enclosed/enclosed areas have a high population abundance compared to open areas. Some possible factors are discussed below.

First, planulae in open waters will be more dispersed, due to the larger area and the higher degree of mixing. Secondly, part of the larval population in open waters may settle in localities of unsuitable depth, thus being lost. Thirdly, a high abundance of medusae in environments with restricted water exchange will also result in a high abundance of planula larvae, and since the larval phase is short (~7 days) it will lead to a high abundance of polyps that will produce a high abundance of ephyrae in the next year. Finally, the other common scyphomedusan in Scandinavian waters, *Cyanea capillata*, is known to be a main predator on *A.aurita* (Båmstedt *et al.*, 1994; Hansson, 1997), and it is not usually found in the non-open environments that are commonly brackish, thereby reducing the mortality of *A.aurita*.

Aurelia aurita thus seems to be a rather flexible species, being able to utilize suitable food conditions for growth and reproduction, and easily adapt to environments with reduced food sources through a reduction in somatic growth, and an allocation of food energy to reproduction. This plasticity in food-energy allocation makes it a strong competitor in diverse environments and explains its worldwide success in coastal waters.

Acknowledgements

The report forms part of a research project financially sponsored by the Norwegian Research Council. We sincerely thank the Ministry of Education, Science, Sports, and Culture, Government of Japan, for a research scholarship to one of us (H.I.) that made this study possible. We also thank Monica Bente Martinussen, University of Bergen, and the staff at the marine biological field station for their help.

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Received on August 26, 1997; accepted on December 1, 1997