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Sexual reproduction of the scyphomedusa *Aurelia aurita* in relation to temperature and variable food supply

Received: 24 June 1997 / Accepted: 23 March 1998

Abstract The effects of food availability and temperature on sexual maturation and female reproductive output of the scyphomedusa *Aurelia aurita* was examined in two populations from the contrasting environments of Southampton Water and Horsea Lake, England. Trends in oogenesis and subsequent reproductive output differed markedly between the two populations. In Southampton Water, the onset of sexual maturation occurred earliest in the larger medusae, but eventually all females became ripe, the smallest being 45 mm bell diameter (BD). The decrease in minimum size at maturity was correlated with increasing temperature. In *A. aurita* from Horsea Lake, size at maturity varied on a seasonal basis, with the smallest ripe female being only 19 to 20 mm BD. There were spring and autumn periods of sexual maturation in this population. During the autumn period, it is likely that food limitation was playing a more critical role in determining medusa size, with decreasing temperature indirectly affecting *A. aurita* by limiting primary and secondary production. In similar-sized ripe medusae, fecundity was greater in Southampton Water, but the planula larvae produced were significantly smaller than those in Horsea Lake. It is suggested that in Horsea Lake, the quality of the larvae are greater in terms of biochemical content to ensure survival of the few gametes produced (i.e. *K*-strategy). Comparison of the reproductive effort of the two *A. aurita* populations revealed that medusae from Southampton Water, which experience greater food availability, are able to direct more energy to reproduction than Horsea Lake medusae. In the latter, *A. aurita* medusae appear to partition the available food resources into either somatic growth (and therefore in-

creased future fecundity) when food is abundant, or reproductive growth when food is scarce.

Introduction

Investigations of the life cycles of cnidarians began with the scyphomedusa *Aurelia aurita* in the early 19th century (Sars 1829). Medusa gonad anatomy and oocyte development are well-known, with studies by Widersten (1965), Chapman (1974), Eckelbarger and Larson (1988), and major reviews by Russell (1970), and Beams and Kessel (1983). Similarly, ecologically/field-oriented research into life-histories (recruitment dynamics, polyp and medusa development) has been carried out by many investigators (Hernroth and Gröndahl 1983, 1985; Hamner et al. 1994; Lucas 1996).

The role of environmental factors such as food, temperature, salinity, and photoperiod has long been considered important in both synchronising annual cycles of reproduction and influencing reproductive output in marine invertebrates (Olive 1985). Evidence is based largely on correlations between gonadal maturation and spawning and one or more environmental variables. In contrast, investigations into the effect of environmental conditions on the reproductive biology of gelatinous predators are not common (Larson 1986; Schneider 1988; Reeve et al. 1989).

Since 1990, the annual cycle of abundance, growth, production, and life-history of *Aurelia aurita* has been described in detail at two sites on the south coast of Britain. Southampton Water is a productive, partially-mixed coastal plain estuary, with typically abundant phytoplankton and zooplankton communities (Lucas and Williams 1994, 1995). Horsea Lake, situated 30 km to the east of Southampton Water is an enclosed, brackish, man-made body of water, characterised by sparse phytoplankton, and a numerically- and species-poor zooplankton community (Lucas 1996; Lucas et al. 1997). These two contrasting systems provide an excellent

Communicated by J.P. Thorpe, Port Erin

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opportunity to examine, in situ, the effect of environmental conditions on the reproductive biology of the neritic scyphomedusa *A. aurita*. The growth, longevity, and maximum size attained by the two populations have already been shown to be greatly influenced by the contrasting food availability at the two locations (Lucas and Williams 1994; Lucas 1996; Lucas et al. 1997).

In Southampton Water, the characteristics of the *Aurelia aurita* population are similar to those of many other western European populations (van der Veer and Oorthuysen 1985; Schneider 1989). Strobilation of ephyrae, indicated by the presence of 1 mm ephyrae starts between late January and mid-March. The single generation of medusae typically remain in the water column until late June, resulting in a longevity of ~100 to 130 d (Lucas and Williams 1994; Lucas et al. 1997). Peak abundance of $< 10 \text{ m}^{-3}$ occurs soon after ephyrae release, declining sharply to $< 1 \text{ m}^{-3}$ in April and to $< 0.5 \text{ m}^{-3}$ from May onwards. Maximum bell diameters (BD) of 120 to 140 mm are attained after a period of exponential growth during May and June. The minimum size at sexual maturity ("ripe" females containing fertilised eggs and planula larvae in brood pouches on their oral arms) reported for Southampton Water is 64 mm BD (Lucas and Williams 1994). This is similar to the minimum sizes of 55 mm BD in laboratory-maintained *A. aurita* medusae (Spangenberg 1965), and 70 mm BD observed in Urazoko Bay, Japan (Yasuda 1971).

In Horsea Lake, the *Aurelia aurita* population is characterised by a 7 mo period of near continuous recruitment, high abundance (25 m^{-3}), small adult size of typically $< 50 \text{ mm}$ BD, and presence in the water column throughout the year. In these respects, this population shares many features with the population in Kertinge Nor, a shallow Danish fjord (Olesen et al. 1994). The medusae are severely food-limited (Lucas et al. 1997). Nevertheless, they are able to reach maturation, and ripe females as small as 19 to 20 mm BD, were observed in 1994. However, these sizes varied considerably on a seasonal basis. It was apparent that when food was scarce, medusae were typically $< 50 \text{ mm}$ in bell diameter and sexually mature. In the two months following a July mesozooplankton peak, both overall size and size at sexual maturity increased. Lucas (1996) suggested that the Horsea Lake medusae were directing food resources into either somatic growth when food was abundant, or reproductive effort when food was scarce.

This paper describes the female reproductive biology of the two contrasting *Aurelia aurita* populations from Southampton Water and Horsea Lake. Information on female gonad index, and oocyte and the size-frequency of planula larvae are combined with existing data (Lucas 1996) on the number of planula larvae present in freshly-captured medusae (an indicator of fecundity). Finally, data on reproductive output are related to previously published values of food availability from the two ecosystems (Lucas and Williams 1995; Lucas et al. 1997), and are summarised in Fig. 1.

Materials and methods

During the quantitative sampling programmes described by Lucas and Williams (1994) and Lucas (1996), *Aurelia aurita* medusae were collected from Southampton Water and Horsea Lake using a 212 μm cod-end plankton net. All medusae were measured across the bell diameter, and wet-weighed after first rinsing with distilled water and careful blotting to remove excess water. Where possible, the sex of each individual was determined. The four horseshoe-shaped gonads were then dissected out of the gastric cavities of the umbrella tissue. In those females that were ripe (containing fertilised eggs and planula larvae in the brood pouches of the oral arms), the oral arms were also cut away from the bell.

In addition to wet weight (WW) of whole medusae, dry weight (DW) and ash-free dry weight (AFDW) of the umbrella and female gonadal tissue were determined. For dry weight, tissue was dried at 60 °C until a constant weight was attained, usually within 2 to 3 d. Ash-free dry weight was measured after 24 h at 550 °C. Gonad indices were calculated for both DW and AFDW, in a similar fashion to that described by Magniez (1983), where gonad index (GI) = (gonad wt:body wt) \times 100.

Gonads and oral arms for histological examination were fixed in Bouin's solution. The tissues were prepared for sectioning using standard ethanol dehydration and paraffin wax-embedding procedures. The wax blocks were sectioned into 7 μm ribbons and stained with Pasini's Triple or Masson's Trichrome stains (Bronte-Gatenby and Beams 1951). Vitellogenic oocytes, which are $> 20 \mu\text{m}$ diam according to Eckelbarger and Larson (1988), and planula larvae were measured across their diameter using the Mocha Image Analysis and Jandel SigmaPro^(TM) software. SigmaPro is highly appropriate if the shape of the object is oval or irregular, as is the case with planula larvae and densely packed oocytes from fecund females. A video-image is frame-grabbed and the circumference of the object defined by the user. Smoothing out of irregularities in the shape of the gamete allows the average, or feret, diameter to be calculated automatically. Feret diameter (FD) is typically smaller but more accurate than measurements obtained using a standard microscope and digitising tablet set-up, as user-bias in identifying the "average" diameter is reduced. For the Southampton Water medusae, which have large, densely-packed gonads and oral arms, a minimum of 50 representative oocytes were measured in each section, and this was repeated in triplicate. Because the Horsea Lake medusae were much smaller and did not contain many oocytes, as many as possible were measured.

Planula larvae production of *Aurelia aurita* from Southampton Water and Horsea Lake has been described by Lucas (1996). Additional samples were collected in 1996 and enumerated using the method described previously by Schneider (1988) and Lucas (1996). The combined results of the two data sets of planula larvae production in Southampton Water are presented.

Oocyte and planula larvae data-sets were tested for normality using the Kolmogorov-Smirnov test. Trends were identified using correlation coefficients and the Mann-Whitney rank sum, Kruskal-Wallis, and Dunn's multiple-comparison tests described by Sokal and Rohlf (1981).

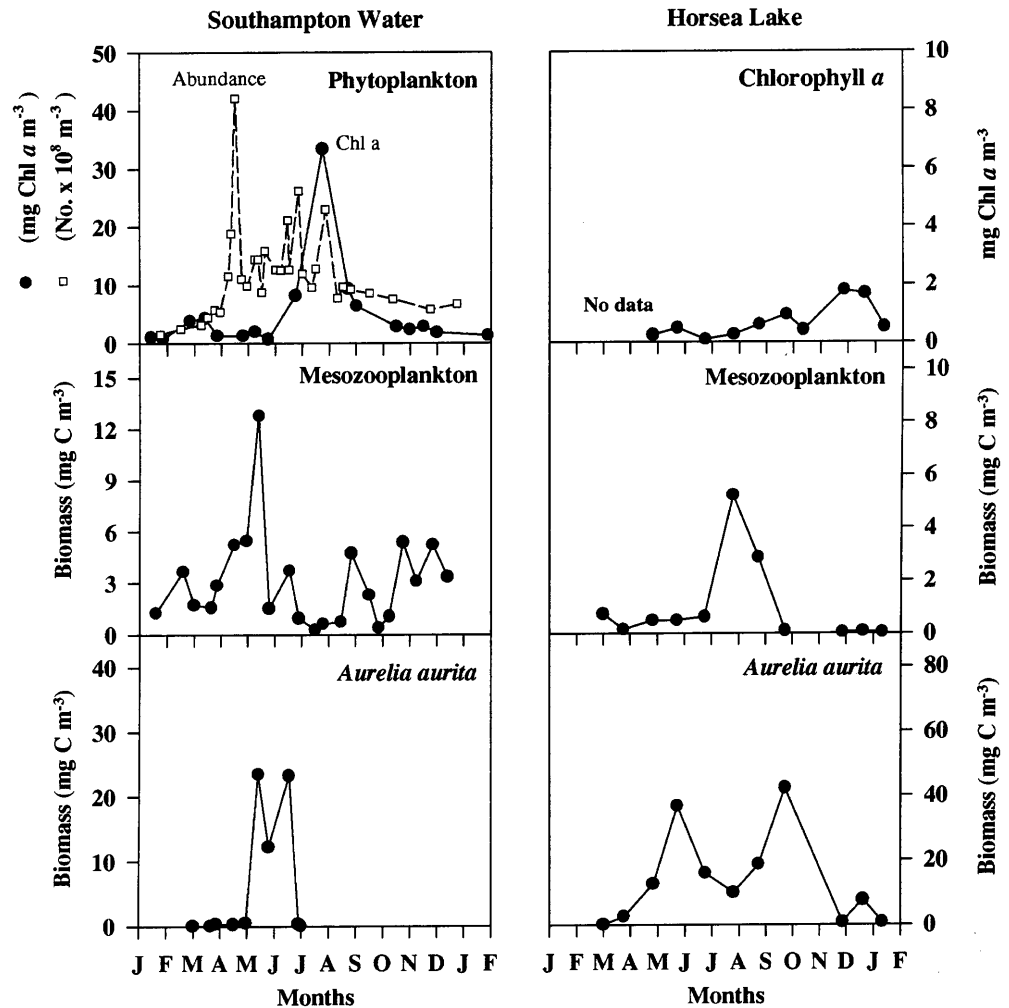
Results

Gametogenesis

Southampton Water

Aurelia aurita is transparent, with clearly visible gonads, allowing the reproductive cycle to be followed easily using a binocular microscope. Separate sexes in this typical univoltine population were first distinguishable in medusae of $> 40 \text{ mm}$ bell diameter at the beginning of

Fig. 1 Plankton dynamics of Southampton Water and Horsea Lake, highlighting contrasting food supply for *Aurelia aurita* in the two ecosystems. (Redrawn from Lucas et al. 1997)



May (Fig. 2). Because of the absence of the gonads in smaller medusae, the gonad index (GI) was calculated only during May and June for Southampton Water. There were no obvious trends with either size or age of the medusae during this period (Table 1). Oogenesis in *A. aurita* is asynchronous. Oocytes at all stages of vitellogenesis occurred simultaneously in all the medusae (60 to 140 mm bell diameter) examined histologically, and both oocytes and planula larvae were present in ripe females. During these months, the *A. aurita* population in Southampton was composed of both ripe and unripe females. At the individual level, differences in oocyte size-composition were identified ($P < 0.001$), with 50% of the individuals differing from the rest of the population ($P < 0.05$). At the population level, there was a slight increase in oocyte size between May and June 1994 ($P < 0.0001$), whilst on an inter-annual basis, variation was insignificant ($P > 0.05$) (Fig. 3).

Ripe females were first observed in late May, 90 to 100 d after ephyrae release, and 1 mo after the water temperature had reached 10 °C; this was a critical period, corresponding to the beginning of exponential growth of *Aurelia aurita* medusae Southampton Water. The onset of maturation occurred earliest in the larger medusae.

For example, on 24 May 1994, the mean (\pm SD) bell diameter of unripe females was 57.8 mm (\pm 20.1) compared with 125.4 mm (\pm 5.5) for ripe females. Later, throughout June, all females sampled were ripe; therefore it appears that all females eventually become ripe, even those of a relatively small size. Maturity does not occur at an definitive minimum size. In 1994, the minimum size to maturity in late May was 118 mm BD, but this had decreased to 89 mm in early June, and 64 mm BD by mid-June. A similar pattern of maturation was observed in 1996, but the smallest female observed to be ripe was 45 mm BD. The seasonal decrease in minimum size to maturity was not found to be related to food availability (see Fig. 1), but was highly correlated with increasing temperature (Fig. 4) (1994: $r = 0.999$, $P < 0.0001$; 1996: $r = 0.999$, $P < 0.0001$).

Horsea Lake

The relative proportions and mean bell diameters of immature, male, unripe female, and ripe female medusae is illustrated in Fig. 5. Two periods of sexual maturity were identified. The first period, May and June, when

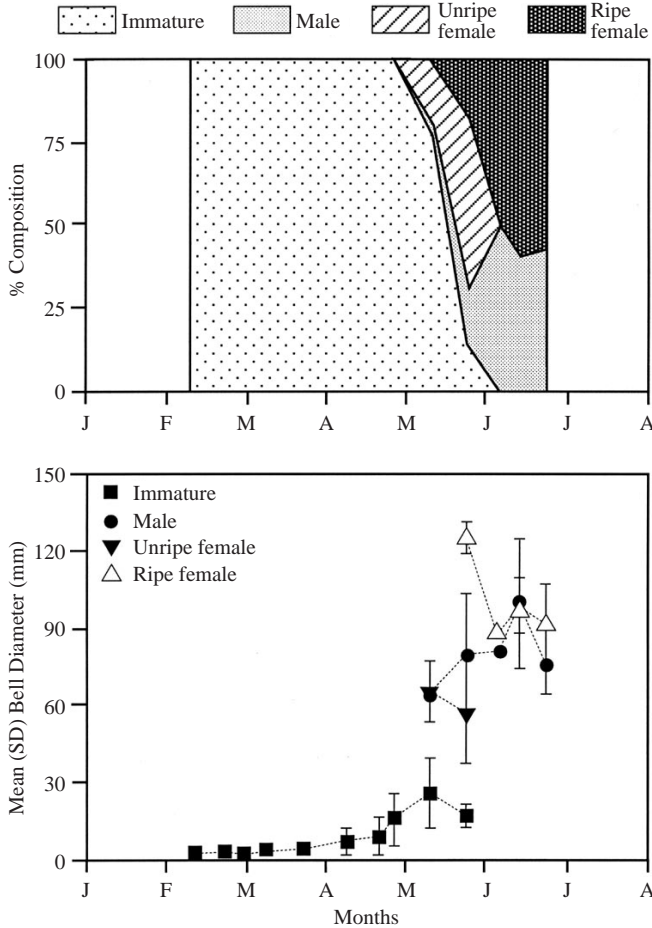


Fig. 2 *Aurelia aurita*. Relative % composition and mean bell diameter of immature, male, unripe female, and ripe female medusae in Southampton Water (11 February to 23 June 1994)

Fig. 3 *Aurelia aurita*. Monthly oocyte size-frequency distributions in Southampton Water. Note that spawning occurs throughout period. Mean bell diameter of medusae used in oocyte measurement is also shown

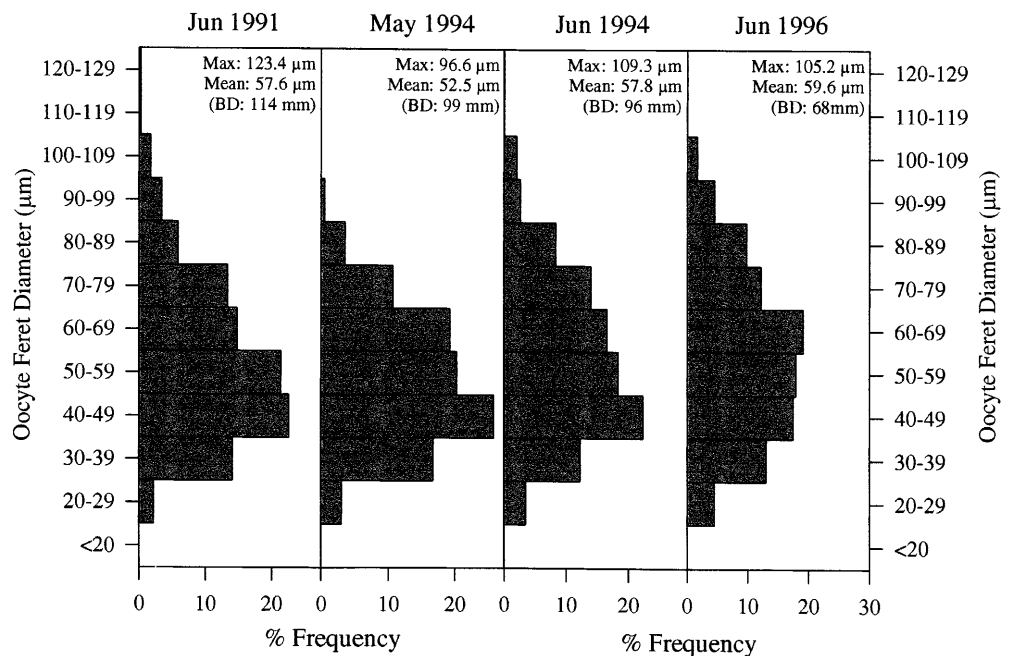


Table 1 *Aurelia aurita*. Mean (\pm SD) monthly dry weight (DW) and ash-free dry weight (AFDW) gonad indices (gonad wt:body wt \times 100) of medusae from Southampton Water in 1996, and Horsea Lake in 1994 (BD bell diameter)

Month	BD (mm)	Gonad indices:	
		DW	AFDW
Southampton Water			
May	92.0 (28.2)	7.52 (2.63)	17.38 (6.53)
June	93.4 (18.7)	8.70 (3.17)	13.06 (5.80)
Horsea Lake			
May	43.9 (6.6)	8.39 (2.58)	10.81 (3.17)
June	45.4 (7.0)	6.76 (3.76)	11.50 (6.78)
July	39.4 (3.6)	8.20 (4.57)	7.35 (3.43)
Aug.	62.6 (16.4)	5.99 (3.83)	7.42 (4.63)
Sep.	72.6 (16.6)	5.44 (2.33)	7.59 (5.01)
Nov.	47.9 (8.1)	6.21 (1.93)	9.11 (4.06)

ripe females accounted for ~30% of female medusae, was followed by a period of increasing bell diameter but virtual absence of sexually mature medusae during July and August. The second period, from September through January, saw ripe females present in increasing numbers until they accounted for all females in November. Longevity is difficult to establish because of the 7 mo period of near-continuous recruitment and the wide temperature range that would affect metabolic and growth rates, but is believed to be ~6 to 8 mo.

Further evidence of seasonal variability in oogenesis was provided by more pronounced trends in the ash-free dry weight gonad index (Table 1) and oocyte size-frequency distributions (Fig 6). Relatively high gonad indices in May and June, coincident with the first period of sexual maturity, were followed by a sharp decrease in July. Values remained low through August and September before increasing in November. As in South-

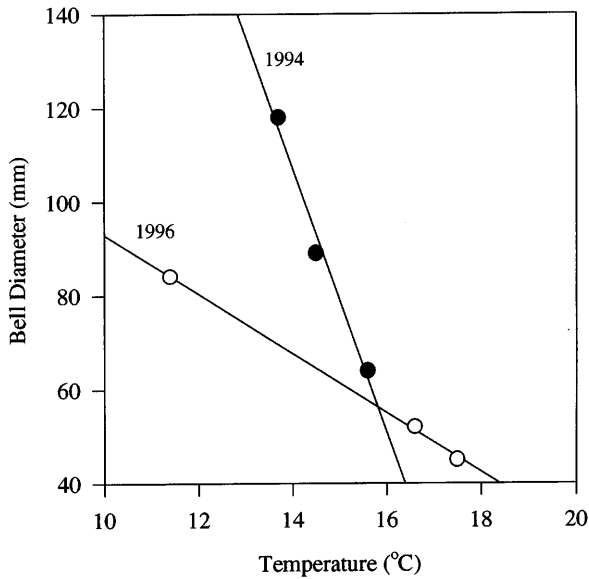


Fig. 4 *Aurelia aurita*. Occurrence of smallest sexually mature female medusae as a function of temperature in Southampton Water [1994: $a = 24.717$, $b = 0.158$, $r = 0.9995$; ($P < 0.0001$); 1996: $a = 17.760$, $b = 0.035$, $r = 0.9991$; $P < 0.0001$]

ampton Water, oogenesis is asynchronous and oocytes and planula larvae occurred simultaneously in ripe individuals. The more complex trends in Horsea Lake meant that there was a high degree of variability in oocyte size composition within the population ($P < 0.001$), with 78% of individuals significantly different ($P < 0.05$). Comparison of the monthly oocyte size-frequencies revealed significant differences between August and May ($P < 0.001$), between September and December ($P < 0.0005$), and between November and December ($P < 0.005$). During the periods of sexual maturation (i.e. May, June, and September through December) gonads contained a wide range of oocyte sizes, and mean oocyte size was typically $> 55 \mu\text{m}$ FD. The period of somatic growth and sexual immaturity in August was clearly demonstrated by a reduction in both the mean and range of oocyte sizes (Fig. 6).

Size at maturity varied greatly (Fig. 7), and paralleled overall bell diameter. During the first period of sexual maturity in May and June, the smallest ripe females were 39 and 25 mm BD, respectively. Following the mesozooplankton peak this increased dramatically to 63 mm BD in August at the start of the second period of maturity. As in Southampton Water, ripe females became smaller throughout the autumn, reaching a minimum of 19 mm in December. Although this decrease in bell diameter was correlated with decreasing temperature (T) ($\text{BD} = 4.436 \times T - 28.321$, $r = 0.940$, $P < 0.01$), it is likely that severe food limitation affected size at maturity during the autumn, and that temperature had an indirect effect by limiting mesozooplankton productivity. Mesozooplankton abundance declined sharply from 4066 m^{-3} in late July to $< 60 \text{ m}^{-3}$ from mid-September through January.

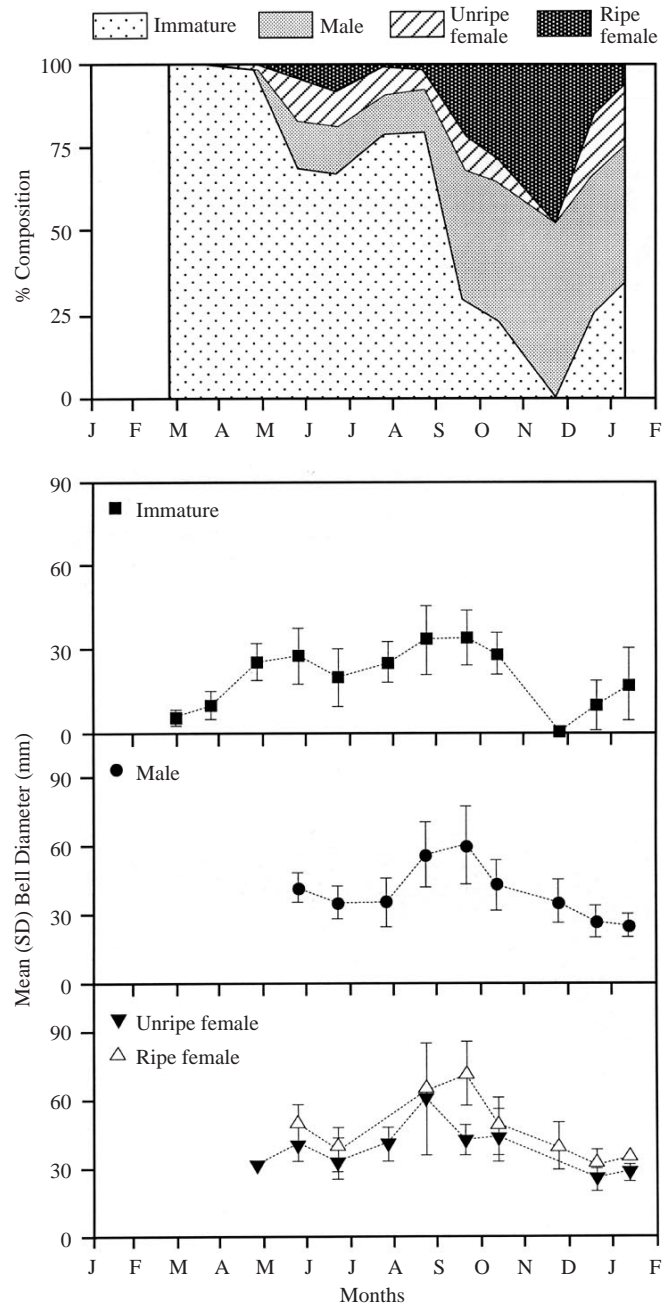
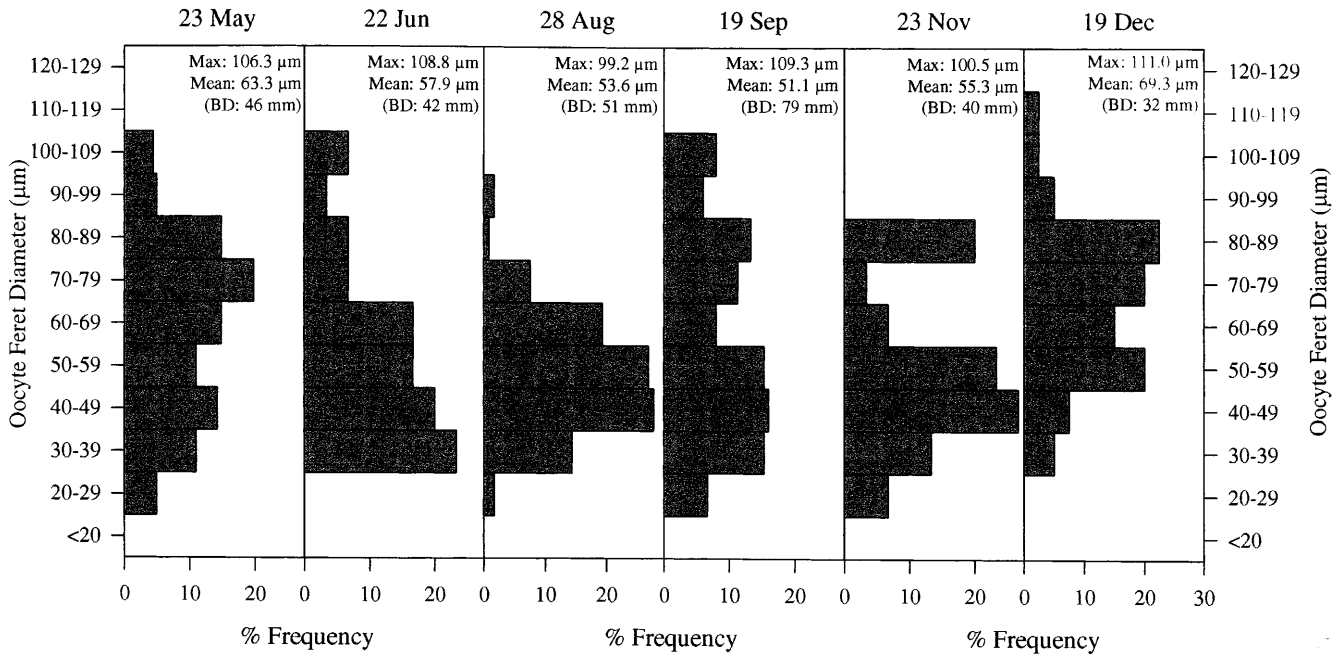


Fig. 5 *Aurelia aurita*. Relative % composition and mean bell diameter of immature, male, unripe female, and ripe female medusae in Horsea Lake (28 February 1994 to to January 1995) (Redrawn from Lucas 1996)

Reproductive output

Southampton Water

Mature oocytes are easily recognised by their large size and pale appearance, compared with early-stage vitellogenic oocytes that stain densely. As previously mentioned, oocytes and planula larvae were found concurrently in ripe females. In such ripe individuals, the largest oocytes ranged between 80.0 and 123.4 μm FD.



Overall, however, mature oocytes were typically > 90 µm FD, and there was no clear trend in mature oocyte size as a function of bell diameter.

Planula larvae measurements during 1991 and 1994 are summarised in Table 2. The total percentage frequency-distribution of planula larvae size-groups illustrated in Fig. 8 reveals a normal distribution. Overall, planula larvae ranged between 20.0 and 59.4 µm FD (mean 34.6 ± 6.1 µm), with no relationship between planula larvae size and bell diameter ($r = 0.319$, $P > 0.05$).

Table 3 shows the mean number of planula larvae in medusae of Southampton Water during 1994 and 1996. Overall, the maximum number of planula larvae counted was 100 767 in a 115 mm medusa. In both years, fecundity increased as a function of medusa wet weight (1994: $r = 0.678$, $P < 0.05$; 1996: $r = 0.522$,

Fig. 6 *Aurelia aurita*. Monthly oocyte size-frequency distribution in Horsea Lake (BD mean bell diameter of medusae used in oocyte measurements)

$P < 0.01$). There was inter-annual variability in this relationship (Table 4), with the smaller ripe medusae in 1996 having more planula larvae.

Horsea Lake

Because sexual maturity of *Aurelia aurita* in Horsea Lake occurs over a long time period (May to January), during which there are considerable differences in food supply and temperature, the current data on reproductive output have been presented on a seasonal basis. The seasonal data also complement previously published data on fecundity (Lucas 1996). The seasons represent time periods before (May to June) and after (August to November) the July peak in mesozooplankton abundance and water temperature (Fig. 1). The winter (December and January) is characterised by mesozooplankton abundance of < 50 m³ and a water temperature of 10 °C. Maximum oocyte and planula larvae sizes and fecundity of pre- and post- mesozooplankton bloom medusae were compared.

Oocytes produced by *Aurelia aurita* in Horsea Lake were similar in size to those in Southampton Water. The largest oocyte measured was 111.0 µm FD (in a 32 mm BD medusa), while in those ripe females containing both oocytes and planula larvae, the largest oocytes ranged between 74.5 and 109.3 µm. In contrast to the similarities in oocyte sizes, planula larvae produced by the Horsea Lake medusae were significantly larger than those from Southampton Water (Table 2) ($P < 0.0001$). Overall, both the size range (24.0 to 71.2 µm FD), and mean size (40.4 ± 7.9 µm FD) were greater, as clearly

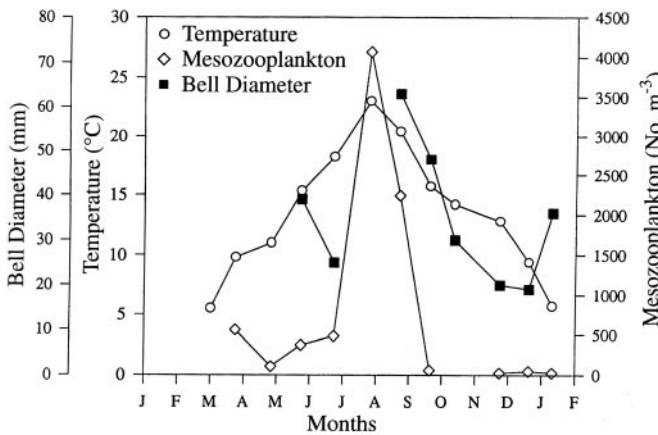


Fig. 7 *Aurelia aurita*. Frequency of smallest sexually mature female medusa as a function of temperature and mesozooplankton abundance in Horsea Lake

Table 2 *Aurelia aurita*. Summary of morphometric measurements of planula larvae from Southampton Water and Horsea Lake. At Horsea Lake, seasons represent time periods before (May to June) and after (August to November) peak of mesozooplankton

Month (year)	BD (mm)	Ferret diam (μm)			
		[n]	min.	max.	mean (SD)
Southampton Water					
June 1991	112.2 (22.1)	[6]	19.96	52.19	34.56 (6.39)
June 1994	111.4 (17.1)	[7]	22.51	59.35	34.67 (5.83)
Overall	111.7 (18.0)	[13]	19.96	59.35	34.61 (6.11)
Horsea Lake					
Pre-bloom	46.0 (9.6)	[3]	24.89	63.36	40.34 (9.25)
Post-bloom	65.2 (14.7)	[11]	24.01	71.22	40.09 (8.36)
Winter	nd (nd)	[0]	nd	nd	nd (nd)
Overall	61.1 (15.7)	[14]	24.01	71.22	40.15 (8.55)

demonstrated in Fig. 8. There were no significant differences in either oocyte or planula larvae production as a function of bell diameter ($r = 0.252$, $P > 0.05$) or time of year ($P > 0.05$).

The relationship between the number of planula larvae present per female at different seasons at Horsea Lake has been reported previously (Lucas 1996). Seasonal differences in fecundity at Horsea Lake were evident (Table 4, updated from Lucas 1996), with the most significant difference between the August to November and December/January periods ($P < 0.01$).

The size of oocytes measured in the present study were somewhat smaller than those published elsewhere because of the method we used, whereby the average (feret) diameter was determined by video-image analysis. Eckelbarger and Larson (1988) reported that late-stage vitellogenic oocytes in *Aurelia aurita* were 175 μm , while Avian and Rottini Sandrini (1991) found that maximum oocyte diameter never exceeded 160 to 180 μm . For

abundance and water temperature in July, while December/January (winter) period is characterised by mesozooplankton abundance $< 50 \text{ m}^3$ and water temperature of 10 $^{\circ}\text{C}$. (BD bell diam; nd no data)

comparative purposes, we made additional oocyte measurements conventionally across their diameter using a digitising tablet and Sigmascan^(TM) software. With this method, the maximum oocyte diameters were 156 μm in Southampton Water and 141 μm in Horsea Lake.

Discussion

Research carried out since 1990 has identified significant differences in many aspects of the population dynamics of *Aurelia aurita* from Southampton Water and Horsea Lake. The role of environmental variables such as food availability and temperature in influencing reproductive characteristics has formed the basis of this work. However, variation in egg number and quality might result from both genetic and environmental factors. Allozyme and morphological differences have been found between other populations of *A. aurita* (Greenberg et al. 1996). Because Horsea Lake has been a virtually isolated system for the last ~ 15 yr, it is recognised that these two populations may in fact differ on a molecular and/or genetic basis, and that this may govern certain population characteristics.

Previous studies by Lucas and Williams (1994) and Lucas (1996) concluded that size at maturity in *Aurelia aurita* was not correlated with either age or size of medusa. The onset of maturation occurs at the upper end of the size range of the population on a given date in both Southampton Water and Horsea Lake, in agreement with the results of both Rasmussen (1973) and Brewer (1989). Thereafter all medusae become ripe, even those of a small size. In Southampton Water this may be the result of increased temperature acting directly on the metabolic rate of *A. aurita* or indirectly on its food supply through increased primary and secondary productivity in the water column. The situation in Horsea Lake is more complex because of the multiple generations and wide range of environmental variables encountered. Although the trend of increasing temperature leading to maturity at smaller sizes applied during the

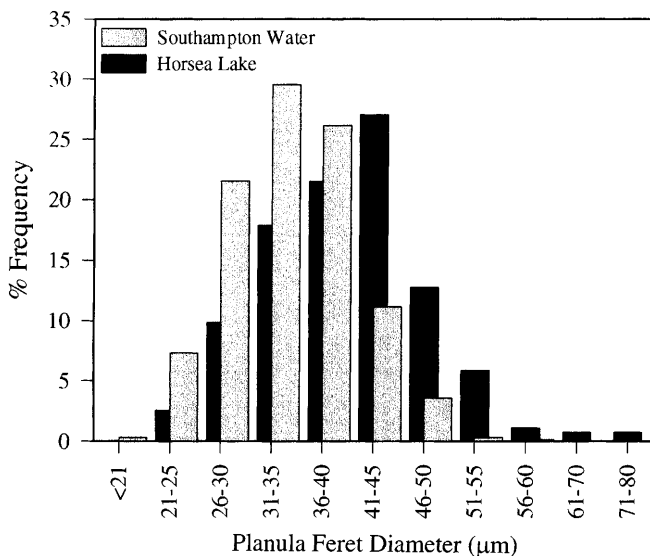


Fig. 8 *Aurelia aurita*. Size-frequency distribution of planula larvae at Southampton Water and Horsea Lake

Table 3 *Aurelia aurita*. Comparison of mean number of planula larvae produced per individual at Southampton Water and Horsea Lake (*Time periods and abbreviations as in Table 2*)

BD (mm)	Southampton Water		Horsea Lake 1994			
	June 1994	June 1996	May–June	Aug.–Nov.	Dec.–Jan.	Overall Average
< 20	nd	nd	nd	nd	nd	nd
20–29	nd	nd	42	159	54	84
30–39	nd	nd	125	233	38	160
40–49	nd	18 320	122	339	317	301
50–59	nd	16 580	356	371	nd	366
60–69	nd	20 180	nd	501	nd	501
70–79	nd	22 647	nd	707	nd	707
80–89	10407	42 583	nd	1 355	nd	1 355
90–99	5670	21 100	nd	4 960	nd	4 960
100–109	17 080	29 050	nd	nd	nd	nd
110–119	63 544	29 080	nd	nd	nd	nd
120–129	26 101	25 280	nd	nd	nd	nd
130–139	23 933	27 700	nd	nd	nd	nd

Table 4 *Aurelia aurita*. Linear regression coefficients for relationship between number of planula larvae produced per individual and wet weight (g), updated from Lucas (1996) (*Time periods as in Table 2*)

Site year	Period	(n)	a	b	r	P
Southampton Water						
1994	June	(10)	246.87	267.25	0.678	0.05
1996	July	(35)	18361.89	103.24	0.522	0.01
Horsea Lake						
1994	May–Jan.	(135)	–80.09	99.30	0.774	0.001
	May–June	(22)	–16.62	60.26	0.649	0.001
	Aug.–Nov.	(96)	–71.54	99.66	0.759	0.001
	Dec.–Jan.	(17)	–57.13	83.72	0.460	0.05

spring spawning-period, the opposite was true during the autumn. It is probable that the extreme food-limitation during the autumn and early winter led to either the precocious maturation of young individuals (Hamner and Jenssen 1974) or shrinkage of existing adult medusae.

The extent to which an organism invests organic matter in reproduction is not fixed, but may vary both with internal state of the organism, i.e. age, and the external state of the environment, i.e. food and temperature, (Calow 1979). Gonad indices, used to assess the reproductive condition of the two *Aurelia aurita* populations in the present study (Fig. 9), reveal that the amount of energy invested in reproduction was clearly much greater in the Southampton Water medusae that are exposed to a more abundant, predictable food supply. Asynchronous oogenesis and differences in size at maturity, however, suggest that continued somatic and reproductive growth are in competition for the assimilated food. This was particularly evident in the Horsea Lake population, in which changes in the gonad index on a monthly basis reflected switches between somatic and reproductive growth associated with changes in mesozooplankton abundance (Lucas 1996). Larson (1986) observed that in the hydromedusa *Phialidium gregarium*, gonads were largest when food was abundant during starvation, they decreased in size rapidly, and egg production stopped within 4 to 10 d. Somatic and reproductive growth in the lobate ctenophore *Mnemiopsis mccradyi* is similarly affected by food supply (Reeve et al. 1989).

Not only does the amount of organic carbon invested into reproduction vary, but also the nature of the partitioning of assimilated carbon once metabolic requirements have been met. Schneider (1988) found that in years of high *Aurelia aurita* abundance (and food limitation), carbon invested into reproduction was low, and there was low fecundity with high organic content per larva. In years of low medusa abundance (and abundant food), carbon invested into reproduction was high, and there was high fecundity with low organic content per larva. Parallels can be drawn with the present investigation. The severely food-limited medusae from Horsea Lake invest less energy into reproduction and produce low numbers of large planula larvae, i.e. *K*-strategy, while medusae from Southampton Water are *r*-strategists, producing large numbers of small larvae. It was anticipated that, following the peak in mesozooplankton abundance in July, together with increased somatic growth of medusae there would be a change in the reproductive output of the Horsea population, so that offspring would be like those of Southampton Water, i.e. smaller and more numerous. This was not observed, and it would appear that the peak in mesozooplankton abundance was not long enough for substantial changes in reproductive output to be sustained. The degree of influence of environmental sources depends largely on conditions experienced by a female during the period that energy is being acquired and converted towards oogenesis.

Most life-history models predict that females with a certain amount of resources available for reproduction

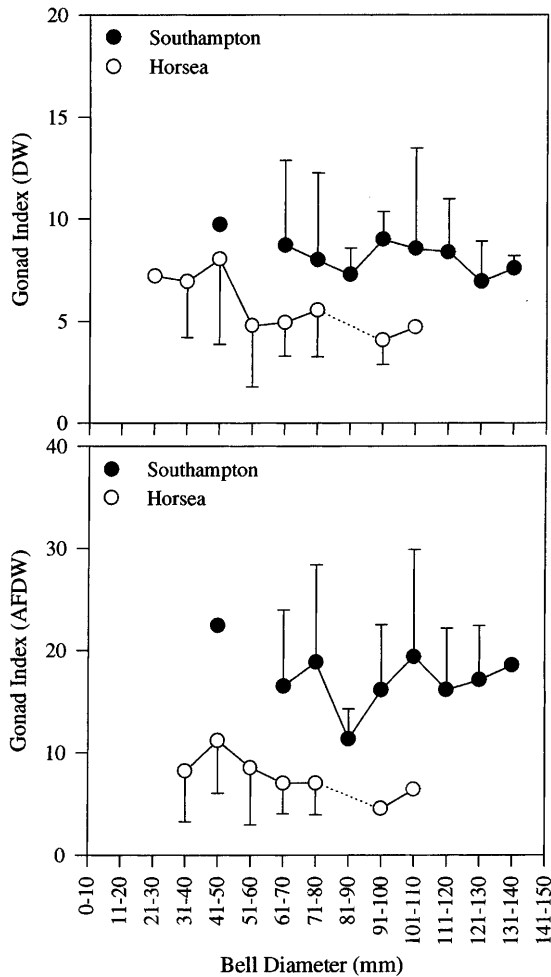


Fig. 9 *Aurelia aurita*. Comparison of dry weight (DW) and ash-free dry weight (AFDW) gonad indices in Southampton Water and Horsea Lake

should produce many small eggs in favourable conditions and fewer, larger eggs in unfavourable conditions (Roff 1992). In the light of the planula larvae measurements in our two study populations, which confirm this prediction, it was somewhat surprising to find oocyte sizes so similar. The inter- and intra-population similarities in oocyte diameter might suggest that oocyte size is genetically pre-determined, but this does not explain how similar-sized oocytes develop into different-sized lecithotrophic larvae. For species such as *Aurelia aurita* with lecithotrophic larval development, the larger the egg, the higher the expected amount of organic material in the egg (McEdward and Chia 1991). If one assumes that the larger the size of a gamete the greater the organic content, then the planula larvae produced by Horsea Lake medusae were of greater quality. This would not seem unreasonable, as the level of investment has been assumed to influence the survival of the offspring (Sibly et al. 1987). All the evidence suggests that under conditions of food-limitation, medusae from Horsea Lake are producing few numbers of high quality lecithotrophic larvae to ensure their

survival to the next stage of development. In the present investigation, apart from oocyte and planula larvae size, gamete quality was not determined for both sites. However, previously published data on the biochemical composition of the gonads of *A. aurita* from Southampton Water, reports mean values ranging from 1.08 to 2.10% carbohydrate, 4.38 to 22.98% protein, and 2.59 to 6.08% lipid, with similar values for ripe oral arms. Eckelbarger and Larson (1988) have provided evidence that three types of storage products are present in vitellogenic oocytes, namely membrane-bound yolk bodies, glycogen, and lipid droplets. Schneider (1988) observed that in years of low planulae production, C:N ratios were high (6.2), indicating a lipid-dominated composition suitable to ensure survival of the offspring, and it is anticipated that this would be the case in Horsea Lake.

The two *Aurelia aurita* populations from Southampton Water, and in particular Horsea Lake, provide an example of how organisms ensure survival of the next generation by adapting to external conditions through changes in reproductive strategy. This helps explain why *A. aurita* has a worldwide distribution in environments with wide ranging temperature, salinity, and food regimes.

Acknowledgements The authors would like to thank Mr. M. Crowfoot and members of the Royal Navy Diving School at Horsea Lake for all their assistance, and for the use of boats throughout the sampling period. Particular thanks also go to Mr. D. Hutchison for the several years of sampling in Southampton Water on the R.V. "Bill Conway". Miss S. Lawes carried out all the oocyte and planula larvae measurements as part of a BSc Honours Project, and Mrs L. Wall provided laboratory assistance for the histological and biochemical work.

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