J. Mar. Biol. Ass. U.K. (2004), **84**, 331–336
Printed in the United Kingdom

Population biology and habitat of the stauromedusa *Haliclystus auricula* in southern Chile

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The population biology and habitat of *Haliclystus auricula* was studied from samples taken every two months in southern Chile between November 2001 and November 2002. A total of 3790 medusae were collected and examined. The abundance of *H. auricula* varied seasonally. Maximum densities occurred in summer (1405/m^2) and minimum densities during the winter, when the population gradually disappeared. Gonads were observed in medusae starting from a size of 2.0 mm. Stauromedusae were found most often on the red filamentous alga *Ceramium rubrum* (69%), followed by *Gymnogongrus furcellatus* (12%) and *Ulva* sp. (10%). There were highly significant differences in mean abundance of medusae on these three algae ($P<0.05$). The remaining 9% of medusae were found on other seaweeds. The smallest medusae (0.08–0.9 mm umbrella height) were found exclusively on *C. rubrum*. The highest densities were recorded in the midlittoral zone.

INTRODUCTION

Stauromedusae are small, stalked, benthic scyphozoans which develop directly from the scyphistoma and live attached to different substrates by means of an adhesive disc on the base of a peduncle. About 45 species are known worldwide, but only 11 have been recorded from the southern hemisphere (Grohmann et al., 1999).

Although stauromedusae are widely distributed, there is limited information on the biology and ecology of these animals, especially in the southern hemisphere. The most detailed studies on this topic were done by Berrill (1962), who observed seasonal cycles in three species from New England, and by Corbin (1979), who described annual population changes in four species at Plymouth, UK.

These scyphozoans have been recorded from a number of different substrates. The most recent records include sand and gravel (Kikinger & von Salvini-Plawen, 1995), rocks and undersides of boulders (Larson & Fautin, 1989; Davenport, 1998), sea grasses (Hirano, 1986a; Larson & Fautin, 1989) and algae [Chlorophyta, Rhodophyta (Zagal & Hermosilla, 2001) and Phaeophyta (Hirano, 1986a,b; Davenport, 1998; Grohmann et al., 1999)]. However, there are no quantitative studies dealing with the habitat of these scyphozoans.

The stauromedusa *Haliclystus auricula* (Rathke, 1806) is distributed on both the eastern and western sides of the North Atlantic (Hirano, 1997). The earliest evidence of this species on the coast off South America comes from medusae collected in the Fitz Roy Channel during the expedition of the Lund University Chile Expedition in 1949 (Kramp, 1961). Later, Amor (1962) reported the stauromedusa on the southern coast of Argentina. Recently, the known distribution of this species has been extended with additional recollections of specimens on the coast of Chile (Quezada, 1970; Zagal & Hermosilla, 2001). In this paper, the population biology and habitat of this species is described from a beach in southern Chile, thus increasing knowledge on the biology and ecology of Stauromedusae.

MATERIALS AND METHODS

The study area is a protected rocky intertidal platform 25 km south-east of Valdivia, southern Chile (39°47′S 73°20′W). At low tides, predominant firm substrates included *Chaetomorpha linum* (Hudson) C. Agardh 1817, *Enteromorpha intestinalis* (Linnaeus) Link 1820, and *Ulva* sp. (Chlorophyta); *Macrocystis pyrifera* (Linnaeus) C. Agardh 1820 (Phaeophyta); *Ceramium rubrum* (Hudson) C. Agardh 1817, *Gelidium lingulatum* Kützing 1868, *Gracilaria verrucosa* (Hudson) Papenfuss 1950, *Grateloupia doryophora* (Montagne) Howe 1914, *Gymnogongrus furcellatus* (C. Agardh) J. Agardh 1851, *Laurencia chilensis* De Toni, Forti & Howe 1920, *Mazzaella laminarioides* (Bory) Fredericq comb. nov. 1993, *Porphyra columbina* Montagne 1845 and *Sarcothalia crispata* (Bory) Leister comb. nov. 1993 (Rhodophyta).

Specimens of *Haliclystus auricula* were collected together with their algal substrates every two months, during low spring tides on Los Molinos beach, between November 2001 and November 2002.

Stauromedusae were collected using 25×25 or 50×50 cm quadrats, which were placed in a surface area of 936 m^2 at 10, 12, 14, 16, 18 and 20 m distances from a predetermined point on the upper shore. The data were normalized to 1 m^2 units.

The species of alga each stauromedusa was found on was identified and recorded. Specimens were preserved in 5% formalin solution after anaesthetization with 1% $MgCl_2$ for about 5 min. The umbrella height of each medusa was measured using a low power binocular microscope. A total of 3790 specimens were collected and analysed.

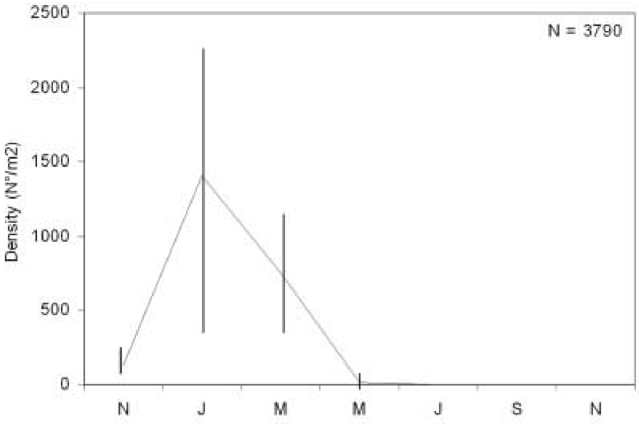

Figure 1. Seasonal variation in density of *Haliclystus auricula* between November 2001 and November 2002.

RESULTS

Population biology

The abundance of *Haliclystus auricula* in the study area was seasonal. The species reached maximum densities in summer (1405/m^2) and minimum densities during the winter, when the population gradually disappeared (Figure 1). The mean density of *H. auricula* during the study was 385/m^2.

Figure 2 shows the seasonal variation of the population structure during the study period. In general, the size frequency of the population presented a negative asymmetric distribution, with a high frequency of small medusae (with a mode of 1.2 mm). The average size of medusae during the study period was 2.08 mm. The smallest and largest individuals observed measured 0.08 and 13.6 mm respectively. Size frequency histograms showed the highest frequencies of large medusae during autumn and spring (with a mode size of 2.3 and 5.3 mm

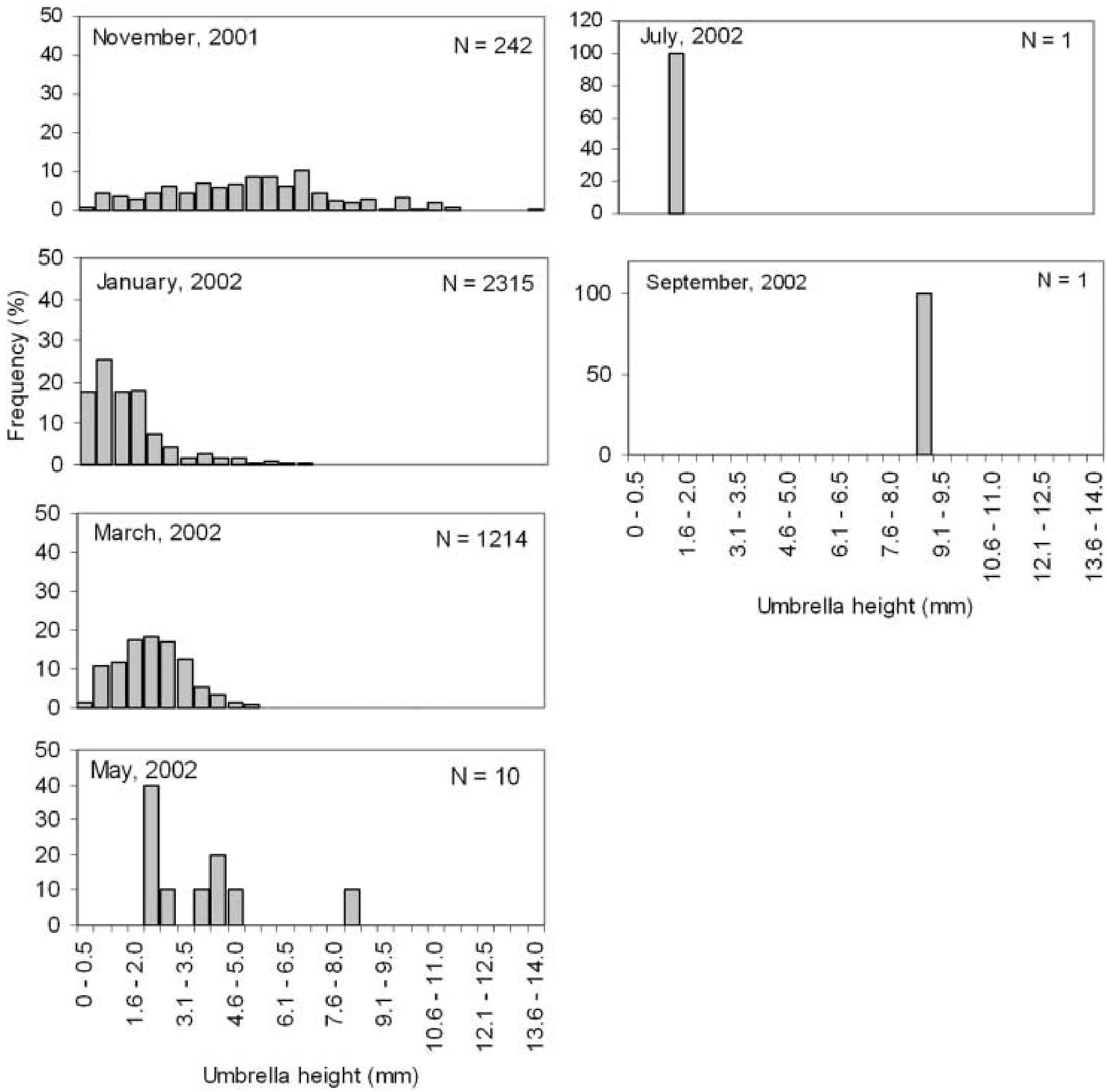

Figure 2. Seasonal variation in the population structure of *Haliclystus auricula*.

https://doi.org/10.1017/S0025315404009233h Published online by Cambridge University Press

Table 1. *Frequency of occurrence (N) and relative abundance (R_a %) of* Haliclystus auricula *on different species of algae at Los Molinos beach, between November 2001 and November 2002.*

Algae substrate	N	R_a %
Class CHLOROPHYTA		
Family ULVACEAE		
Ulva sp.	378	9.97
Family CLADOPHORACEAE		
Chaetomorpha linum (Müller) Kützing, 1845	13	0.34
Class PHAEOPHYTA		
Family DESMARESTIACEAE		
Desmarestia ligulata (Lightfoot) Lamouroux, 1813	2	0.05
Class RHODOPHYTA		
Family GELIDIACEAE		
Gelidium lingulatum Kützing, 1868	33	0.87
Family HALYMENIACEAE		
Grateloupia doryophora (Montagne) Howe, 1914	123	3.25
Family PHYLLOPHORACEAE		
Gymnogongrus furcellatus (C. Agardh) J. Agardh, 1851	456	12.03
Family GRACILARIACEAE		
Gracilaria verrucosa (Hudson) Papenfuss, 1950	5	0.13
Family GIGARTINACEAE		
Mazzaella laminarioides (Bory) Fredericq comb. nov., 1993	20	0.53
Sarcothalia crispata (Bory) Leister comb. nov., 1993	20	0.53
Family CERAMIACEAE		
Ceramium rubrum (Hudson) C. Agardh, 1817	2623	69.21
Family RHODOMELACEAE		
Laurencia chilensis De Toni, Forti & Howe, 1920	117	3.09
TOTAL	3790	100%

Table 2. *Summary results of a one-way analysis of variance on log transformed mean abundance of* Haliclystus auricula *on the algae* Ceramium rubrum, Gymnogongrus furcellatus *and* Ulva *sp. during spring and summer.*

Source of variation	Sum of squares	Degrees of freedom	Mean square	*F*-ratio	*P*-value
Between groups	5.4755	2	2.7377	8.37	0.0008
Within groups	15.6911	48	0.3269		
Total	21.1666	50			

respectively), with the highest frequencies of small medusae recorded during the summer (mode size of 1.4 mm).

Stauromedusae with visible gonads were frequently observed during spring and the end of summer, starting from a 2.0 mm size. During November 2002, no stauromedusae were observed.

Habitat

Haliclystus auricula was found on 11 species of algae (Table 1). The medusae were most frequently found on the rhodophytes *Ceramium rubrum* (69%) and *Gymnogongrus furcellatus* (12%), and on the chlorophyte *Ulva* sp. (10%). There were highly significant differences in the mean abundance of the medusae on these three algae ($P<0.05$) (Table 2). Mean abundances of medusae on the algae *C. rubrum* and *G. furcellatus* were significantly different at a 95.0% confidence interval, as well as mean abundances on *C. rubrum* and *Ulva* sp. No significant differences were recorded in mean abundances of medusae on the algae *G. furcellatus* and *Ulva* sp. (Table 3).

Table 3. *Summary results of Tukey multiple comparison between log transformed mean abundance of* Haliclystus auricula *on three different algae, during spring and summer (levels containing ×'s in the same column form a group of means within which there are no statistically significant differences; * indicates statistically significant differences).*

Method: 95.0%	Count	Tukey HSD mean	Homogeneous groups	
Gymnogongrus furcellatus	17	1.01445	×	
Ulva sp.	17	1.21417	×	
Ceramium rubrum	17	1.78752		×

Contrast	Difference	± Limits
C. rubrum–G. furcellatus	*0.77307	0.47434
C. rubrum–Ulva sp.	*0.57335	0.47434
G. furcellatus–Ulva sp.	−0.19973	0.47434

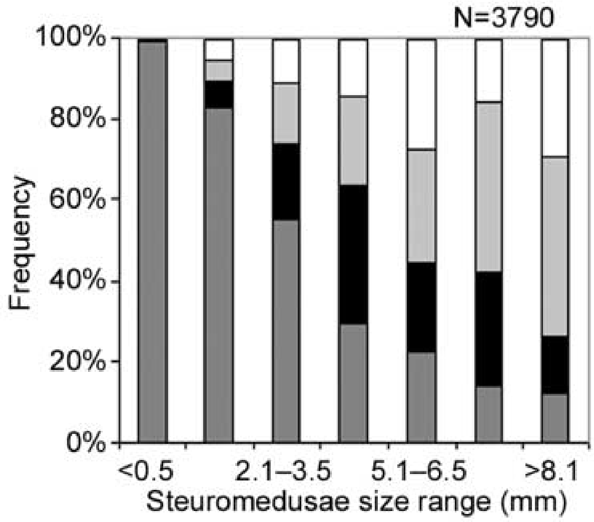

Figure 3. Population structure of *Haliclystus auricula* on different species of algae between November 2001 and November 2002. white bars, other; light grey bars, *Ulva* sp.; black bars, *Gymnogongrus furcellatus*; dark grey bars, *Cerumium rubrum*.

The smallest medusae of the population sampled (0.08–0.9 mm umbrella height) were found exclusively on the red filamentous alga *C. rubrum*, whilst the rest of the size frequencies were observed on all three species of algae (Figure 3).

The mean densities of stauromedusae in the supralittoral, midlittoral and infralittoral zones were 184/m^2, 670/m^2 and 301/m^2, respectively.

DISCUSSION

Seasonal variations in the abundance of *Haliclystus auricula* concur with the observations of Uchida (1929), Gwilliam (1956), Corbin (1979) and Hirano (1986a) for the same species. This seasonality may be related to the availability of suitable algal substrates. The period of highest stauromedusa abundance, during spring and summer, coincided with periods of greatest algal cover. High medusa abundances recorded during the summer indicate optimal conditions for growth and nutrition during this period. The appearance of smaller size-classes of stauromedusae during the summer indicate a peak period in larval recruitment. Throughout winter, environmental conditions are probably least favourable to *H. auricula*. Increased wave action was evident in the study area, with a considerable amount of dead algae found on the beach. Some of the thalli had dead stauromedusae on their surfaces.

Densities of medusae recorded in this study most certainly represent an underestimate of the actual population size. Stauromedusae may be hard to observe because of their small size and because they usually acquire the same colour as their algal substrate. This is especially true for the smallest medusae, which could only be observed using a microscope. No other records of stauromedusa density have been published and the high abundances recorded in this study cannot be compared with those of other areas.

The population reached its highest density during the summer period, when there was a great abundance of juveniles, and decreased drastically during winter months, eventually dropping to zero. This indicates that the life cycle of *H. auricula* is completed in a year, in accord with Corbin's (1979) observations.

The life cycle of Stauromedusae includes a very small, creeping planula larva lacking cilia (Otto, 1976), and medusae disappear completely from the intertidal zone during winter. How can this huge increase in the population size during spring and summer be explained?

In the past, Sars (1846) observed seasonal population changes in the stauromedusa *Lucernaria quadricornis* O.F. Müller 1776 on the Norwegian coast. He implied that the medusa migrated seasonally from the littoral zone into deep water, which would account for its absence during some seasons of the year. Gwilliam (1956) observed the disappearance of *H. auricula* during winter months in western North America. He examined a large number of *Zostera* blades (where medusae had previously been attached) during part of the spring and found no signs of an encysted phase. He also took plankton tows through the *Zostera* bed when the animals first started to appear, but no planulae were ever recovered. Gwilliam thought that a permanent subtidal population existed in the vicinity which could continually supply planulae, and when conditions were suitable these planulae would settle and mature on the sea grasses. Upon reaching sexual maturity such medusae would provide more larvae, so the population could build up over the summer.

No evidence of seasonal migration was found during this study. No stauromedusae were observed in deeper waters whilst SCUBA diving in winter, when the population had disappeared from the intertidal zone.

Otto (1978) observed that as *Haliclystus* planulae settle, they often aggregate and are surrounded by an amorphous sheath of nearly hexagonally packed subunits enclosing the planulae. She suggested that these settled, aggregated planulae constitute an overwintering stage. It is not surprising that Gwilliam (1956) did not find any encysted phase or planulae considering that the planula of *Haliclystus* measures about 100 μm in length (Otto, 1976) and is surely hard to find in nature.

Although no planulae or cysts of stauromedusae were observed in this study, *Haliclystus* planulae probably do not develop directly after settlement in nature but form cysts during unfavourable conditions. This would explain the absence of a winter population. However, further research is needed in this area.

During the study period, the highest densities of stauromedusae were recorded in the midlittoral zone. Desiccation limits the upper distribution of most sessile intertidal organisms, including hydroids (Calder, 1991; Henry, 2002), so it is not surprising that the density of *H. auricula* decreased at higher shore levels. Distribution limits of hydroids may also be influenced by wave action and be determined by larval preferences for settling in zones where macroalgal assemblages provide the thickest canopy (Henry, 2002). The midlittoral zone probably presents the most favourable physical and biological conditions for survival of stauromedusae on the beach studied.

However, the lower distribution limit of the area studied was constantly the lower tide limit except for sampling during winter months, when tides were rarely so low because of rough water conditions including wind, rain, poor visibility, and greater wave action. Therefore, the densities recorded for this zone may have been under-estimated due to sampling difficulty.

Haliclystus auricula has been observed in the past on rhodophytes (Amor, 1962), the rhodophyte *Gracilaria* sp. (Quezada, 1970), the phaeophyte *Sargassum* sp. (Uchida, 1929; Hirano, 1986a), and the sea grass *Zostera marina* Linnaeus 1758 (Uchida & Hanaoka, 1933; Gwilliam, 1956; Berrill, 1962). Unfortunately, no quantitative observations were undertaken as part of these studies, so no comparisons can be made with the results presented here.

The fact that the smallest medusae were found exclusively on the red filamentous alga *Ceramium rubrum* suggests selection and preference for this habitat on Los Molinos beach during settlement and metamorphosis of the stauromedusa. Gonads were observed in medusae with a size greater than 2.0 mm. Beyond this size, the medusae were observed on other algae besides *C. rubrum* (Figure 3). As the stauromedusa grows and becomes sexually mature, it may become too heavy for the alga it is on and it moves to another substrate where it may attach itself more firmly, such as *Gymnogongrus furcellatus* or *Ulva* sp.

Several studies have reviewed larval settlement and the association of serpulid polychaetes, bryozoans, and hydroids with algal substrata (Scheltema, 1974; Seed, 1985). The selection of substrate during larval settlement and the survival of adult colonies may be determined by a combination of biological factors such as seasonality and abundance of the substrate (Llobet et al., 1991), chemical, physical and biological nature of the substrate (Ryland, 1974), reproductive strategies (Boero, 1984; Seed, 1985), competition for space (Seed, 1985; Calder, 1991; Llobet et al., 1991), food availability (Boero, 1984) and predation (Calder, 1991), as well as physical characteristics in the environment including water movement (Boero, 1984; Seed, 1985; Gili & Hughes, 1995), sedimentation (Boero, 1984; Seed, 1985), light, exposure to air, salinity, temperature, and pollution (Boero, 1984; Gili & Hughes, 1995).

All of these factors should be considered in evaluating habitat selection of Stauromedusae in future studies. They should be addressed particularly during the moment of settlement of stauromedusan larvae, since this is the time when selectivity probably takes place. Future studies will probably confirm or broaden the spectrum of algal substrata presented in this work, and substrate selection may vary geographically.

I am most grateful to Y. Hirano for preliminary identification of the stauromedusa, and for her help and advice. Special thanks go to C. Hermosilla and J. Harries for their assistance in the field, J. Jaramillo for help during identification of algae, and to my advisors C. Jara, E. Clasing and J. Zamorano for their support during the completion of my undergraduate thesis. I also thank D. Ashby (National Marine Biological Library), F. Boero, D.R. Calder, J. Davenport, D. Fautin, L.A. Gershwin, S. Goshima, C. Gravili, L.-A. Henry, Y. Hirano, C. Mills, J. Otto, R. Scheltema, and R. Seed for sending references used in this paper and T. Roberts for reviewing the manuscript.

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Submitted 30 June 2003. Accepted 6 January 2004.