AN ABSTRACT OF THE THESIS OF

<u>Thomas M. Heitstuman</u> for the degree of <u>Master of Science</u> in <u>Oceanography</u> presented on <u>June 30, 1994</u>. Title:<u>Aspects of the Biology and Culture of Scyphomedusae of</u> the Oregon Coast

Abstract approved:____Charles B. Mille

Charles B. Miller

Field and laboratory work was undertaken in 1993 to increase understanding of the life history and ecology of the brown jellyfish, *Chrysaora fuscescens*, a large semaeostome typically abundant in the neritic regions of the Oregon coast during summer months. Few medusae were found during 1993, possibly the result of anomalous conditions caused by an El Niño event in that year. Benthic scyphozoan polyps (scyphistomae) were discovered in Yaquina Bay, Oregon, during an extensive underwater survey of the bay using SCUBA. The distribution of the scyphistomae appears to be related to the availability of suitable substrate, almost exclusively the rockwork of jetties and breakwaters, suggesting human activity may be largely responsible for periodic "blooms" of scyphozoan jellyfish.

Based upon (1), a study of the scyphistomae's nematocyst complement and (2), a rearing experiment of the juvenile medusae (ephyrae) produced by polyps collected while undergoing strobilation, the Yaquina Bay polyps were determined to be the benthic stage of the moon jelly, *Aurelia aurita*, a species with a worldwide distribution. Attempts to induce metamorphosis and strobilation in the polyps using techniques developed elsewhere were unsuccessful, suggesting that there may be differences in the cues that trigger metamorphosis in *Aurelia* collected from various regions.

Aspects of the Biology and Culture of Scyphomedusae of the Oregon Coast

by

Thomas M. Heitstuman

A THESIS

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Charles B. Mille

Professor of Oceanography in charge of major

Jawrence A Small

Acting Dean of the College of Oceanic and Atmospheric Sciences

Dean of Graduate School

Date thesis is presented _____ June 30, 1994

Typed by researcher for _____ Thomas M. Heitstuman _____

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TABLE OF CONTENTS

I. INTRODUCTION	1
Scyphozoan life cycle - a brief account	3
II. DESCRIPTION OF YAQUINA BAY	6
III. METHODS	12
Diving operations	12
Yaquina Bay	12
Offshore	15
Lab Work	16
Tank series	17
Planktonkreisel	20
Care and feeding	21
Identification of scyphistomae	23
IV. RESULTS	25
Field findings	25
Lab findings	29
Strobilation initiation	31
Identification	32
V. DISCUSSION	37
Field work	37
Lab work	39
VI. CONCLUSIONS	42
BIBLIOGRAPHY	44

LIST OF FIGURES

<u>Figure</u>

Page

1.	Typical scyphozoan life cycle	4
2.	1989 seawater temperatures at R/V WECOMA pier	9
3.	1993 seawater temperatures at R/V WECOMA pier	10
4.	Blue water diving apparatus	13
5.	Yaquina Bay, Oregon	14
6.	Tank series and planktonkreisel	18

LIST OF TABLES

Tal	ble	Page
1.	Identification of Chesapeake Bay polyps	24
2.	Search effort	26
3.	Nematocyst complement	35

ASPECTS OF THE BIOLOGY AND CULTURE OF SCYPHOMEDUSAE OF THE OREGON COAST

I. INTRODUCTION

Much remains to be learned about the ecology of scyphozoan medusae, particularly in the eastern Pacific (review by Larson 1990), although several workers have demonstrated their importance in planktonic ecosystems generally. It is known, for example, that scyphozoans exert significant predation pressure on zooplankton and may be the dominant influence on species composition in some marine communities (Huntley & Hobson 1978, Möller 1978, 1980; Feigenbaum & Kelly 1984). Predation by medusae may be particularly important for fish populations (Möller 1980, 1984; Arai & Hay 1982, Bailey & Batty 1983, 1984; Shushkina & Musayeva 1983). Other gelatinous zooplankton are preyed upon by scyphomedusae (Arai & Jacobs 1980, Feigenbaum & Kelly 1984. Larsen 1986, Strand & Hamner 1988), and this predation may indirectly improve survival of some shellfish larvae (Purcell et al Finally, symbiotic relationships between scyphomedusae, 1991). particularly *Chrysaora* spp., and some hyperiid amphipods, juvenile crabs, and small fishes are common (Mansueti 1963, Harbison et al

1977, Laval 1980, Larson 1990) and likely significant to pelagic processes overall.

I report here a study of one of the more common scyphozoans along the Oregon coast, *Chrysaora fuscescens*. Commonly known as the brown jellyfish or the brown sea nettle, *C.fuscescens* is a large semaeostome. It is typically present at high densities in our neritic surface waters during the summer. Shenker (1984) reported *C. fuscescens* swarms exceeding 1800 liters of medusae per 10^5 m^3 , containing at least 80% as much carbon (50 mg C m⁻³) as the densest copepod concentrations reported off Oregon. However, little is known of the life history, ecological relationships, or grazing pressure exerted by this species. My goal has been to extend this knowledge.

One notable gap in the literature is information on the habitat of the sessile phase, the scyphistoma, of *C. fuscescens*. Shenker's work with *C. fuscescens*, and work by Cargo and Schultz (1966, 1967) with its east coast congener, *C. quinquecirrha*, suggest Oregon estuaries may be important in the reproductive biology of the species. Off Oregon and Washington Shenker (1984) found (his figure 3) the greatest densities of *C. fuscescens* nearshore, with particularly high numbers off the entrances to estuaries (Yaquina Bay, Columbia River). Cargo and Schultz mapped the geographic

range of the scyphistomae of *C. quinquecirrha* in Chesapeake Bay. They found scyphistomae in only those regions of the estuary where salinities ranged from 7 to 20 ‰, where depths were less than 11m, and where suitable substrate -- oyster shell "boxes" -- was present. Perhaps the scyphistomae of *C. fuscescens* has similar requirements.

My goals in this study were to find *C. fuscescens* scyphistomae in the wild, positively establish their identity, roughly delineate the limits of their distribution, and learn something about habitat cues that may trigger various events in their life cycle (strobilation, encystment, etc.). On the whole my work concentrated on Yaquina Bay (44°35'N 124°04'W).

Scyphozoan life cycle - a brief account

The scyphozoan life cycle (figure 1) typically includes a conspicuous medusal stage that reproduces sexually, with zygotes hatching as free-swimming, ciliated larvae (planulae). The planulae attach to suitable substrates and develop into small (order 2mm), inconspicuous polyps (scyphistomae). The scyphistomae are typically able to reproduce asexually by stolon formation, budding or longitudinal fission. Eventually the scyphistoma undergoes a series

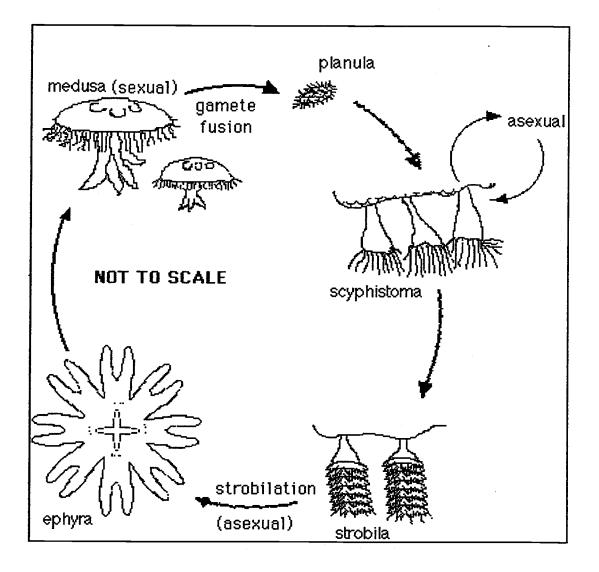


Figure 1. Typical scyphozoan life cycle

of transverse constrictions in which it, now called a strobila, comes to resemble a stack of saucers. The "saucers" develop and eventually detach (a process called strobilation) to produce freeswimming juvenile medusae (ephyrae). Scyphistomae typically encyst as winter approaches and emerge in the spring to strobilate again. Medusae seldom survive the winter.

Although their scyphistomae remain unidentified in the field, the Monterey Bay Aquarium (MBA) has been rearing *C. fuscescens* (including scyphistomae) for several years with good success (Sommer, 1992). Scyphistomae were obtained by *in vitro* fertilization utilizing excised gonadal tissue from several netcaptured medusae.

II. DESCRIPTION OF YAQUINA BAY

Yaquina Bay is Oregon's fourth largest estuary and a prominent feature of the central Oregon coast (44°35'N 124°04'W). The bay is the drowned valley of the Yaquina River, which drains a small section (627 km²) of coastal mountain range. Several communities are situated on the bay. The largest, Newport, is a small city located near the mouth of the estuary and serves as a port for a large commercial and sport fishing fleet. Yaquina, about six kilometers from the bay entrance, is a rural village on the outskirts of Newport. About 20 kilometers up the bay is Toledo, the second largest community in the area after Newport. Toledo is the site of a large Georgia-Pacific Corporation Kraft process pulp mill. Still farther up the bay is the village of Elk City. Elk City is commonly taken to be the upstream limit of tidal influence in Yaquina Bay.

The channel leading up Yaquina Bay is periodically dredged to a depth of 9.1 m between the entrance and the turning basin at McLean Point and then 5.5 m from McLean Point to Yaquina.

A monsoonal weather pattern dominates the central Oregon Coast. Heavy winter rains, intermittent rains during spring and fall, and drought during the summer are typical. This results in a pronounced annual cycle of river flow and, consequently, a

pronounced annual cycle of salinity distribution in the bay. Seasonal changes in the prevailing winds likewise are responsible for seasonal changes in the surface flow of the nearby Pacific Ocean. During the late fall, winter, and early spring, winds are predominantly from the east and south resulting in northerly and onshore Ekman flow of surface water. The situation is reversed during the summer with winds from the north and west resulting in southerly and offshore Ekman flow of surface water. The result is periods of strong upwelling during most summers, with cold nutrient-rich subsurface (200-300m) water surfacing in the nearshore regions of the Oregon coast. A summertime increase in solar radiation accompanies the upwelling of cold water resulting in a very damped annual temperature cycle in the coastal ocean and in the lower reaches of the Yaquina Bay.

Yaquina Bay experiences a mean diurnal tidal range of 2.4 m and a maximum range of about 3.8 m. Approximately 70% of the water in the large embayment near Newport is exchanged each tidal cycle. The large volume of water moving with each tide produces high velocities and thorough vertical mixing, ensuring little difference in the bottom and surface temperatures and salinities during most of the year in the lower bay (Miller 1983). Exchange in the upper bay depends upon freshwater flow. Heavy rains during the

winter can result in freshwater sweeping across the surface of the bay creating marked gradients in both temperature and salinity.

The 1993 weather patterns off the Oregon coast, indeed around the world, were affected by an El Niño event. Record levels of snow and rain fell in Oregon during the first half of the year. A change in the normal surface winds failed to drive significant upwelling during the spring and much of the summer. With no upwelling occurring, unusually warm sea surface temperatures were found along our coast. The 1992/1993 El Niño event was particularly anomalous in that it was actually the second year of a two-yearlong El Niño event that began in 1991. In contrast, 1981, the year Shenker sampled *C. fuscescens* populations off Oregon's coast, was a more typical, non-El Niño year.

Figures 2 and 3 depict year-long records of seawater temperature (daily maximum, minimum and mean) at the R/V WECOMA pier located near the Hatfield Marine Science Center on Yaquina Bay. The thermistor measuring the temperature is located about 3.5m off the bay's bottom (about 2m below mean lower low water) at the pier. Figure 2 represents water temperatures in the bay during 1989, a non-El Niño year (data was not available for 1981). Mean temperatures during the late spring and early summer, from May to July, hovered around 12°C, with water temperatures

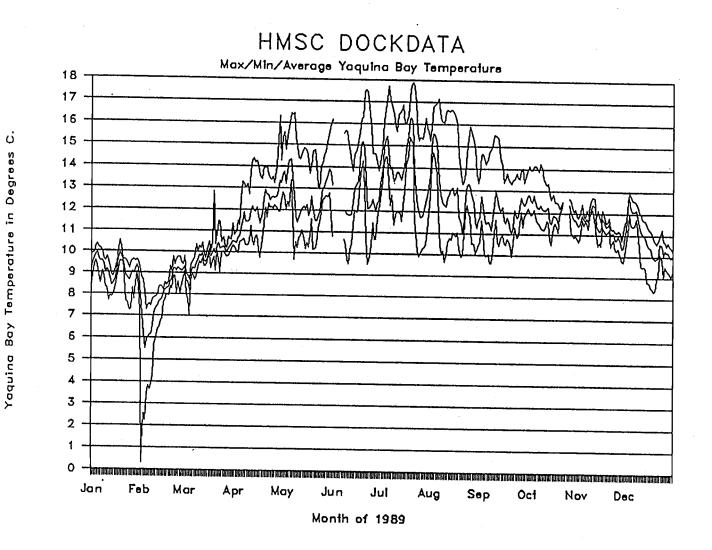


Figure 2. 1989 seawater temperatures at R/V WECOMA pier

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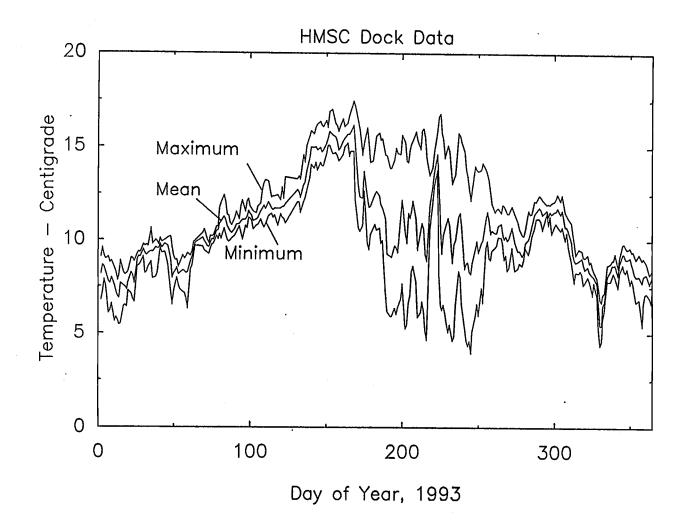


Figure 3. 1993 seawater temperatures at R/V WECOMA pier

rarely above 15°C. Figure 3 shows similar data for 1993. The mean temperature between days 140 and 175 (mid-May to mid-June) is near 15°C with a daily maximum of about 17°C during the period. The difference between the two years can be explained in light of the El Niño event and coastal upwelling. During a typical year (1981, 1989) upwelling cold, nutrient-rich subsurface water in the nearshore regions of the coast damps seasonal temperature increases in the lower bay. During El Niño years, however, temperatures in the lower bay are not damped by cold, upwelled water and are thus significantly higher.

It is interesting to note that as the El Niño event ended midsummer of 1993, vigorous upwelling apparently followed resulting in colder than normal temperatures in the lower bay.

III. METHODS

Diving Operations

An extensive search for scyphistomae of *Chrysaora fuscescens* was undertaken by SCUBA diving. Diving in and around Yaquina Bay was performed using standard SCUBA equipment and procedures. Blue water dives were also conducted to search for medusae. These were also made with SCUBA equipment, but using techniques described by Heinle (1985). Figure 4 illustrates the rig employed during blue water dives. The descent line and diver tending lines allowed an acceptable level of safety while conducting offshore dives. The rig ensured maintenance of diver orientation by providing a visual frame of reference otherwise lacking in deep water. The rig also ensured that divers were tethered and unable to drift off; thus were able to devote their full attention to the observations at hand.

Yaquina Bay

Approximately 40 dives were conducted in and around Yaquina Bay. Figure 5 and table 2 indicate the locations of the dives. Most dives were conducted in low visibility conditions. Low water

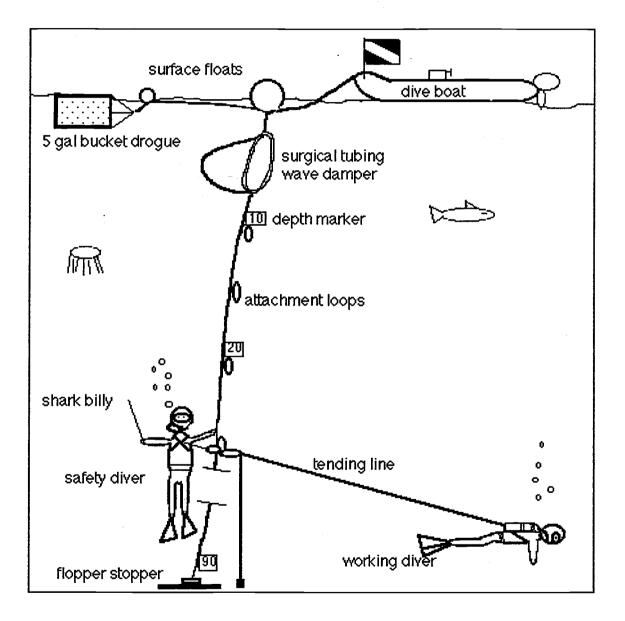
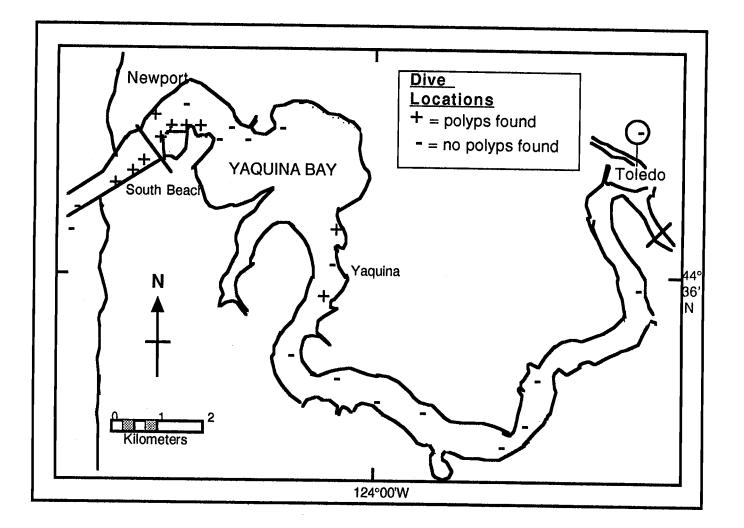


Figure 4. Blue water diving apparatus



temperatures and strong currents posed additional challenges. Most dives entailed searching for scyphistomae with little indication as to where they might live, especially during the dives early in the A typical dive lasted about 45 minutes. project. During that time my diving partner and I would swim slowly along the bottom examining the sediment, rocks, shells, algae, and any debris for polyps. Equipped with lights, we would carefully search the cracks and crevasses of rockwork, pilings and docks. If poor visibility prevented positive identification of a suspected polyp a sample would be returned to the lab for identification. Although the area that could be searched during the course of a dive depended upon the bottom type, typically several hundred yards along a meandering path could be examined.

Offshore

A half dozen dives were conducted in the nearshore waters off Yaquina Bay from small Coast Guard boats and four additional dives were performed at locations off the Washington Coast from small boats attached to the R/V WECOMA (cruise W8908A, 2-10 August 1993). During a typical blue-water dive we would descend to the bottom of the deployed diving rig (figure 4), stop and observe any visible plankton for several minutes, ascend 3-5m and stop to observe again repeating the process until we reached the surface.

Lab_Work

Aquarium systems of two types were constructed to allow for the maintenance of *Chrysaora* through the various stages of its life cycle. Three series of three 37.7 liter (10 gallon) acrylic tanks were constructed to rear scyphistomae and newly-released ephyrae under several temperature/salinity combinations. A 250 liter planktonkreisel was built to rear juvenile through adult medusae. All tanks (with the exception of holding tanks used at the Hatfield Marine Science Center) were of a continuous circulation, closedsystem design utilizing an artificial seawater mixture and a multistage filtration system.

The aquarium systems were set up in a refrigerated "cold" room in the basement of Burt Hall II on Oregon State University's main campus. Use of the cold room obviated the need for tank chillers to maintain near-normal seawater temperatures in the tanks.

Tank series

(See figure 6) The tank series were constructed of commercially-available 37.7 liter acrylic tanks. Glass tanks would have been an acceptable alternative but would have been more difficult to modify to accommodate the required plumbing.

PVC piping and fittings were used for much of the plumbing due to its low toxicity. Silicone tubing was used when possible at locations where a flexible hose was required. Although the silicone tubing used was very low in toxicity, it was also quite flaccid, necessitating the use of stiffer, but perhaps more toxic polyethylene tubing for sump uptake hoses and water inlet lines. The sump and CaCO₃ trickle filter were fashioned from opaque white high density polyethylene (HDPE) food service containers. The filtration systems for the tank series and the planktonkreisel were Marineland $^{\ensuremath{\mathbb{R}}}$ "Magnum 350" canister filter pumps (350 gallon/hour maximum) with integral floss sleeves to remove particulates and activated charcoal canisters to adsorb organic contaminants. Wet/dry "trickle" filters were constructed and filled with approximately 10 kgs of medium grade coral hash to serve as a substrate for nitrifying bacteria. The theory (Spotte 1979a, b) is that the bacteria colonize the coral surfaces and oxidize ammonium wastes to less toxic

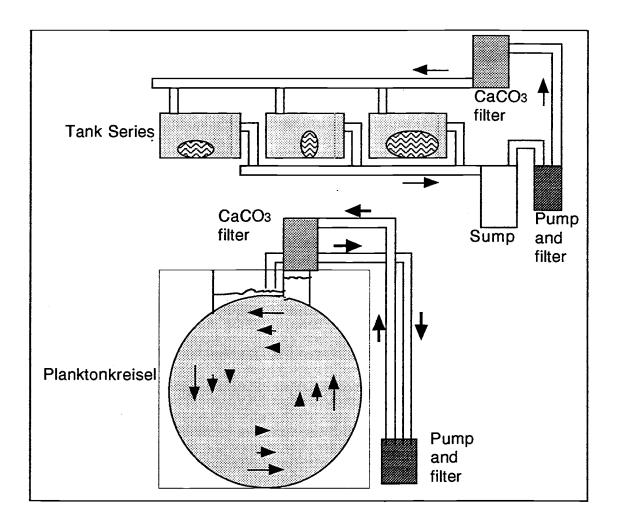


Figure 6. Tank series and planktonkreisel

nitrites and nitrates. The coral hash also serves to buffer pH changes as organic wastes accumulates in the tanks. Partial water changes were performed periodically (about 10% monthly) to maintain good water quality.

A sump was incorporated into each of the tank systems, except the kreisel, to facilitate partial water changes. The sump also served as a reservoir for the seawater, allowing the pumps to be shut off without the risk of overflowing the tanks during feeding or in the event of a pump malfunction or power failure. The design of the tank made the sump unnecessary in the planktonkreisel system.

Miscellaneous acrylic cement, Teflon tape, and aquarium grade silicone glue were used as necessary in each system. Considerable care was exercised to remove or minimize use of any material that could have deleterious effects on marine organisms. No metal parts were used. All components were cleaned without the use of detergents, rinsed well in distilled water, then finally rinsed with distilled/deionized water.

All tanks were covered with acrylic tank tops to minimize evaporation and lessen the possibility of inadvertent contamination. A 75W incandescent lamp with timer supplied low level light to the far side of the tank room for 12 hours each day. Each series of tanks was provided with a fluorescent lamp for detailed observations of

tank inhabitants. The fluorescent lamps were used only for limited times, usually much less than one hour per day).

Artificial seawater was produced by mixing Coralife Scientific Grade Marine Salt[®] and distilled then Milli-Q deionized water according to the manufacturer's instructions. Specific gravity was measured with a hydrometer. Salinity was computed using a nomogram derived from the International Equation of State for seawater (Fofonoff & Millard 1983).

A framework was constructed in front of the tank series to support a binocular microscope horizontally, allowing detailed observations of the scyphistomae in the tank series without removing them from their individual tanks.

Planktonkreisel

I had a planktonkreisel fabricated by a small plastics company, Flair Plastics of Portland, Oregon, based upon the design of Hamner (1990). The 101.5 cm diameter, 30.5 cm wide, 250 liter planktonkreisel was designed for maintenance of relatively large scyphomedusae, permitting careful observation of its gelatinous inhabitants.

The clever design of the planktonkreisel (figure 6) makes it a

nearly ideal aquarium in which to maintain and observe gelatinous zooplankton. Central to the design is the circulation pattern and velocity gradient that is established in the tank. Water circulates in a vertical vortex, with relatively rapid flow along the perimeter of the tank decreasing to nearly zero flow in the tank's center. This flow pattern tends to keep the inhabitants off the bottom and away from the sides, simulating actual conditions in the planktonic environment. Another important element of the planktonkreisel design is that the incurrent jets direct water flow across the topside drain screen, sweeping it clean and preventing delicate planktonic organisms from being trapped against it and perhaps injured or killed. Finally, the tank's black background and side lighting provide a large, dark-field-illuminated volume, allowing observation of structural details normally transparent in transmitted light (Hamner, 1990).

Care and Feeding

Three independent tank series sets were constructed as described above then filled with artificial salt water. The first tank series, series A, was maintained at 14°C with a salinity of approximately 30%. Series B, was maintained at 8°C and 20%

salinity. Finally, series C and the planktonkreisel were maintained at 8°C and 30‰ salinity.

Scyphistomae and ephyrae were fed newly-hatched brine shrimp (Artemia salina) nauplii (usually less than 24 hours old) until most scyphistomae were contracted and distinctly rose-colored. This was accomplished in the tank series by temporarily securing the pumps and pipetting 2-5ml of Artemia (concentrated in seawater) in the immediate vicinity of the scyphistomae, stirring as necessary to ensure all scyphistomae were at least exposed to them.

Temperatures were monitored regularly, as was the specific gravity in each tank. Distilled/deionized water was added as necessary to maintain salinity.

The sole source of nutrition for the polyps, ephyrae and medusae was Artemia salina nauplii hatched from cysts (Ocean Star International Inc., Red Jungle Brand, Pro 80, Snowville, Utah). The cysts, collected from the Great Salt Lake, Utah were hatched nearly continuously to provide food for the polyps and medusae in culture. Cysts were incubated for about 24 hours in well-aerated, 25°C artificial seawater to obtain a nearly 100% hatch rate. The newlyhatched nauplii were then concentrated and immediately fed to the scyphistomae, ephyrae or juvenile medusae; or cooled to 8°C and used within 24 hours.

Identification of scyphistomae

Calder utilized differences in the nematocyst complement of both scyphistomae (Calder, 1971) and ephyrae (Calder, 1977) to help differentiate between *Chrysaora, Aurelia* and *Cyanea* in Chesapeake Bay. Calder (1971) found that the presence or absence of several different types of nematocysts in the polyp could differentiate the three genera (table 1). *Aurelia* polyps contained only microbasic heterotrichous euryteles and two types of atrichous isorhizas, "a"-atrichs and oviform polyspira nematocysts. *Chrysaora* polyps also contained euryteles and "a"-atrichs and occasionally another type of nematocyst, holotrichous haplonemes. Finally, *Cyanea* polyps contained only euryteles and atrichous isorhizas of the "a"-atrich the "alpha"-atrich types.

<u>Genus</u>	microbasic heterotrichous <u>eurytele</u>	a-atrichous <u>isorhiza</u>	polyspira atrichous <u>isorhiza</u>	alpha-atrichous <u>isorhiza</u>	holotrichous <u>haploneme</u>
Aurelia	+	+	÷	-	-
Chrysaora	2 +	+	-	-	+
Cyanea	+	+	-	+	-

Table 1.Identification of Chesapeake Bay polyps by nematocysttypes (after Calder 1971)

IV. RESULTS

Field Findings

No *C. fuscescens* medusae were found in, or in the immediate vicinity of, Yaquina Bay. Only a few were found in the nearby Pacific Ocean during the course of this study. Attempts to locate the medusae included numerous surface (from small boat) and subsurface (SCUBA) searches (table 2). The attempts themselves were somewhat sporadic and unsystematic. Weather, availability of small boats, and scheduling demands on my and my diving partner's time limited opportunities for searches. Anecdotal evidence gathered during discussions with local mariners; fishermen, coastguardsmen, and the crew of the R/V WECOMA, tended to confirmed our limited observations. Nearly everyone we spoke with indicated that they had noticed fewer medusae during the summer of 1993 than in previous years.

I was able to collect only two specimens of *C. fuscescens* (a total of four were seen from the ship's deck) during WECOMA cruise W8908A from 2 to 10 August 1993 off the Oregon and Washington coasts. One specimen (approximately 7cm bell diameter - unflattened.) was apparently healthy. The other (approximately 8cm

Table 2. Search effort

P=plankton tow, D=dive, B=beach/shore search, S=surface search from boat or ship

Date	Location of search Poly	ps/medusae?	Type of search/comments
4/20/93	Btwn markers 21 & 45	no	P
6/25/93	Btwn LNG tank & marker 42		P ·
6/26/93	Inside end of s. jetty	no	D
6/26/93	Oregon Oyster Co. dock	no	D
6/27/93	Weiser Point	no	D
6/27/93	5 nm off Newport	no	S/ search for medusae
7/2/93	Boat ramp 1 nm s. of Toledo	no	D
7/3/93	Rocks under WECOMA pier	yes/polyps	B/ minus tide
7/3/93	Mouth of Boone Slough	no	D
7/4/93	Mudflats e. of LNG tank	no	B/ minus tide
7/4/93	Rock/mud bch n. of Yaquina	no	B/ minus tide
7/4/93	Beach near marker 25	no	B/ minus tide
7/4/93	Mouth of Boone Slough	no	B/ minus tide
7/4/93	3 nm s. of buoy "Y"	no	S/D
7/4/93	Under WECOMA pier	yes/polyps	D/ to 2 ft below MLLW
7/9/93	Middle groin of s. jetty	no	D
7/9/93	Municipal pier	no	D
7/10/93	S. Beach Marina w. bkwtr	yes/polyps	D/10-15 ft below MLLW
7/10/93	Outside tip of s. jetty	no	S/D
7/16/93	1/2 mile s. of Boone Slough	no	D
7/16/93	HMSC pier	no	D/night dive
7/17/93	8-10 nm off Newport	no	S/D
8/3/93	46°45N 124°30W	no	S/D
8/4/93	46°45N 124°30W	yes/medusae	S/D/observed several
			medusae from surface but
			none during dive
8/5/93	46°45N 124°45W	yes/medusae	S/D/collected 2 medusae on
			surface with dipnets
8/6/93	46°45N 125°01W	no	S/D
8/9/93	10nm offshore to Newport	no	S
9/9/93	Middle groin, s. jetty	yes/polyps	D
9/16/93	Weiser Point	yes/polyps	D/11-19ft below MLLW
9/20/93	Buoy 26	no	D
9/20/23	Buoy 30A	no	D
9/21/93	Coast Guard docks	yes/polyps	D/attached to plastic bucket
9/21/93	Buoy 9	no	D _
9/21/9	Buoy 11	no	D
9/28/93	N. brkwtr, S. Beach Marina	yes/polyps	D
9/29/93	Easternmost groin s. jetty	yes/polyps	D
10/9/93	2 westmost groins s. jetty	yes/polyps	D
10/10/93	Middle groins s. jetty	no	D/photo dive
10/10/93	Sawyers Landing dock	yes/polyps	D/undersides of dock
10/11/93	Marina near buoy 47	no	D/undersides of dock
10/11/93	Great Bend Marina	no	D/undersides of dock

Date	Location of searchPo	olyps/medusae?	Type of search/comments
10/11/93	Toledo City docks	no	D/undersides of dock
10/11/93	Dock 2 mile e. of Toledo	no	D/undersides of dock
10/11/93	Boat landing w. of Elk City	no	D/undersides of dock
10/11/93	Dock at Elk City	no	D/undersides of dock
2/2/94	WECOMA pier	yes/polyps	D/collected polyps for tanks
2/2/94	Coast Guard docks	yes/polyps	D/collected polyps for tanks
2/2/94	Sawyers Landing Dock	yes/polyps	D/collected polyps for tanks
2/20/94	WECOMA pier	yes/polyps	D/collected polyps for tanks
3/19/94	Middle groins s. jetty	no	D/photo dive
4/28/94	WECOMA pier	yes/polyps	B/collected during minus tide
5/7/94	4nm off Newport	yes/medusae	P

.

Table 2. Search effort (cont.)

bell diameter - unflattened) was found alive but moribund and lacking any trace of oral arms or other subumbrellar structures. This second specimen also harbored a small crab symbiont. Cargo (1972) noted a similar moribund condition and absence of subumbrellar appendages for some *C. quinquecirrha* in the wild but had no suggestions as to possible causes.

Scyphistomae were found near the bay entrance between the jetties and as far up the Yaquina Bay as Weiser Point (figure 5), although during many dives no scyphistomae were found at all. . Nearly all scyphistomae were found on the undersides of rocks in interstices with little fouling. Of the scyphistomae found attached to rocks, all were found below the mean lower low water (MLLW) mark, ranging from about 0.3m to 10m below MLLW. During one particularly low spring tide series, I found many scyphistomae under the WECOMA pier exposed by the tide. I collected several rocks with the polyps and transferred them to lab tanks. They appeared to suffer no adverse effects from their brief exposure to air.

In several instances scyphistomae were found in areas other than the undersides of rocks. On the north side of the bay, east of the Yaquina Bay bridge under the U. S. Coast Guard Station's docks, we found a polyethylene food service bucket lying on its side with a dense collection of scyphistomae suspended from the top of the

inside surface of the bucket. In another instance, in a shallow location (approximately 1m below MLLW) between two of the groins on the south jetty, we found a number of scyphistomae scattered on a small vertical rock face with moderate algal fouling. Finally, we found several scyphistomae near Yaquina at Sawyer's marina on the underside of a polystyrene dock float with moderate to heavy fouling (primarily algae and hydroids).

Several medusae were captured during a short plankton tow 4 nautical miles off Newport in May 1994, possibly suggesting the summer of 1994 may produce greater numbers of *C. fuscescens* medusae than in 1993.

Lab Findings

I collected rocks bearing many scyphistomae, some of them strobilating, in February, 1994 from the subtidal rockwork at the foot of the R/V WECOMA dock adjacent to HMSC on Yaquina Bay. Polyp-bearing rocks collected from the same location in April, 1994 bore no strobilae. I was able to successfully maintain scyphistomae and strobilae in the series tanks. Ephyrae released from the strobilae, however, did not fare as well in the series tanks, probably as a result of predation by the scyphistomae (Sommer, 1992). Upon transfer to the planktonkreisel, the ephyrae survived better but mortality was still high. Only four, of 18 ephyrae transferred to the planktonkreisel, survived for the four months until the experiment was ended. During this period the ephyrae grew slowly but steadily, increasing from 1-2mm to about 25mm in bell diameter over the four months -- a growth rate of about 0.2mm/day.

Feeding was inexact for the scyphistomae in culture. Some polyps were probably starved, others overfed. With flow through the tanks stopped, concentrated *Artemia* nauplii were pipetted into the vicinity of the rock(s) bearing the scyphistomae. The tanks were then stirred or otherwise agitated to ensure the scyphistomae had adequate opportunity to capture *Artemia* prey. Despite my efforts to ensure every individual polyp was adequately fed, for some scyphistomae it was difficult to maintain recurring contact between predator and prey. Scyphistomae in other areas in the same tank, those located near the tank floor for instance, apparently always had a ready supply of *Artemia* at hand to eat, the individual polyps being quite plump and rose-colored.

Little is known of possible predators on scyphistomae. At one point during this study I discovered that an aeolid nudibranch, *Hermissenda crassicornis*, had devoured nearly every polyp from several rocks (as well as those growing on a small floating section

of plastic bucket) being maintained in a 37.71 (10 gallon) holding tank at Oregon State University's Hatfield Marine Science Center (HMSC) in Newport, Oregon. Cargo & Schultz (1967) observed similar predation by a nudibranch of the genus *Coryphella* on polyps of *C. quinquecirrha*.

Strobilation Initiation

I did not observe the spontaneous initiation of strobilation, that is, a scyphistoma undergoing metamorphosis to a strobila, in any of the scyphistomae I collected. All ephyrae that were released into my laboratory tanks were from strobilae collected as such. The lack of strobilation initiation may have been a result of deficiencies in diet, the time of collection and season of captivity, or lack of requisite stimuli, perhaps a temperature, salinity, or photoperiod cue. Polyps were maintained in the lab at several different temperature/salinity combinations without any noticeable differences. There was little apparent difference in the success of strobilation between strobilae maintained at 30‰ and those maintained at 20‰ salinity (both at 8°C). The 30‰ tank had a much larger number of ephyrae produced, about fifty compared to the dozen or so produced in the 20‰ tank, but it also had many more strobilae, perhaps five to ten times as many than the 20‰ tank. Attempts to initiate strobilation in scyphistomae by adding 100µg/liter and later 1mg/liter of potassium iodide (KI), both with and without preconditioning at lower temperatures, as described by Spangenberg (1967) for *Aurelia* had no effect (30‰ /14°C tank series).

Identification

Considerable uncertainty existed as to the proper identification of the scyphistomae discovered. Although they were certainly scyphozoan, and undoubtedly of the order Semaeostomeae, it was possible that the polyps were any of a half dozen or so genera common to Oregon waters. The most likely candidates were *Chrysaora fuscescens, Aurelia aurita, Cyanea capillata, Pelagia colorata,* and *Phacellophora camtschatica*.

Gross anatomical comparisons between *C. fuscescens* scyphistomae received from the Monterey Bay Aquarium (MBA), *Aurelia aurita* scyphistomae from the Oregon Coast Aquarium (OCA), and the scyphistomae collected in Yaquina Bay provided little clue as to the identity of the Yaquina Bay scyphistomae. The MBA scyphistomae were rather large, fleshy and slightly rose colored.

Each bore 16 fleshy tentacles. Most OCA scyphistomae bore 16 tentacles, but their numbers varied from 16 to 24. They were quite rosy, and the tentacles were finer than those from MBA. The Yaquina Bay scyphistomae were white, most had more than 20 tentacles, usually 22 to 24, though some contained only 16. The tentacles on the Yaquina Bay scyphistomae varied from short and thick to very long and fine. Certainly coloration of the scyphistomae depends upon the prey items consumed by the scyphistomae, here Artemia nauplii for laboratory reared specimens. Scyphistomae from the field and those starved in the lab were white. Feeding substantial quantities of Artemia always resulted in rose-colored scyphistomae. The coarseness of the tentacles may also be related to prey type or abundance. The number of tentacles is more likely to be characteristic, but the simple anatomy and variable morphology of scyphistomae make definitive identification on this basis alone uncertain (Calder 1971). Laboratory culture of scyphistomae likely introduces additional variability in morphology (Cargo, 1972).

Upon microscopic examination of the nematocysts of scyphistomae collected under the R/V WECOMA pier, under the Coast Guard Station dock and from the underside of a Sawyer's Landing dock (all had been in the lab for several months), all were found to contain microbasic heterotrichous euryteles and atrichous isorhizas

of the "a"-atrich type (table 3). Another type of atrichous isorhiza, the polyspira, was found in nearly all polyps examined (table 3). These three nematocyst types are the same complement Calder found for *Aurelia* in Chesapeake Bay, and certainly suggests the Yaquina Bay scyphistomae are *Aurelia*. It is, however, impossible to entirely rule out differences in the nematocyst complement of Pacific Ocean and Chesapeake Bay species of each genus.

My attempt to rear the ephyrae produced by Yaquina Bay polyps (strobilae) to adult medusae in order to establish positive identification was more definitive. Like scyphistomae, scyphozoan ephyrae are similar and difficult to identify to genus with much certainty. Newly-released Yaquina Bay ephyrae, about 2mm in diameter, resembled the description of Aurelia ephyrae by Russell (1970) in the number of gastric cirri, but a key characteristic, the shape of the distal ends of the interradial canals was intermediate between Russell's descriptions of Aurelia and Chrysaora. Further. the ephyrae lacked a definite ring canal characteristic of Aurelia. As the juvenile medusae entered the post-ephyral stage (6-7mm diameter), however, the ring canal began to develop, closely resembling Larson's (1976) description of Aurelia post-ephyrae. Still later (10-12mm diameter), the development of numerous short marginal tentacles, ribbon-like oral arms, eight rhopalia, and

Table 3. Nematocyst complement

Date	Origin of polyps	# polyps	# w/ eury	a-atr.	poly.	_alpha-atr	haplo.
4/21/94	CG dock - bucket	1	1	1	1	0	0
	Sawyers Landing dock	1	1	1	1	0	Ō
	WECOMA dock - rock	1	1	1	1	0	0
4/26/94	WECOMA dock - rock	3	3	3	3	0	0
4/29/94	OCA - Aurelia polyps	3	3	3	3	0	0
	OCA - unknown polyps	3	3	3	3	0	0
6/14/94	OCA - Aurelia polyps	10	10	10	10	0	0
	WECOMA dock - rock	10	10	10	10	0	0
	CG dock - bucket	10	10	10	10	0	0

eury. = microbasic heterotrichous euryteles

a-atr. = "a"- atrichous isorhiza

poly. = polyspira atrichous isorhizas

alpha-atr. = "alpha"-atrichous isorhizas

haplo. = holotrichous haplonemes.

branched radial canals leave little doubt as to the medusa's identity -- it is almost certainly *Aurelia*. As the animals reached about 2cm diameter their marginal tentacles were quite long, about equal to the radius of the bell of the medusae, surprisingly long for *Aurelia*.

Taken together, the scyphistomae nematocyst complement and the morphology of the post-ephyral and juvenile medusal stages, it is certain that the polyps collected in Yaquina Bay are *Aurelia*.

V. DISCUSSION

Field Work

C. fuscescens medusae were conspicuously absent from the nearshore region of Oregon's central coast during the summer of 1993. My work here did little to explain their absence, hence I have few facts to constrain speculation. One obvious explanation for the absence would be the failure of the year's reproductive output. Reproductive failure during 1993 might be attributed to the anomalous weather patterns during the year. An El Niño weather pattern persisted for a second year during 1993 resulting in warmer than average surface temperatures, increased rainfall and reduced upwelling of nutrient-rich water. Shenker's work during a massive "bloom" of C. fuscescens was conducted during the summer of 1981, a non-El Niño year, typical of most years off the Oregon coast. Could high sea surface temperatures, increased rainfall levels and low salinities, or other unusual factors related to regional climate have failed to trigger strobilation or decreased survivorship of medusae during the spring and summer of 1993?

Cargo and King (1990) developed a model for forecasting the abundance of *C. quinquecirrha*, in Chesapeake Bay. They found that

streamflow in the Chesapeake Bay watershed during January through June and the water temperature during several critical time periods were the most important factors in predicting the forthcoming summer's abundance of sea nettles. Streamflow is related to total runoff (rain, snow, etc.) during the period. Apparently unusually high temperatures in January and high salinities in February delay protective encystment of the sessile polyp, delaying excystment and thus strobilation in the spring. Similarly, low temperatures in May delay strobilation of the scyphistomae. In both cases the year's ephyrae production is delayed, resulting in reduced survival, perhaps related to food or other physiological requirements not being met (Cargo & King 1990).

Though it is tempting to attribute 1993's low abundance of *C. fuscescens* to 1993's unusual weather here, evidence of cause and effect is lacking. Other workers (review by Barber & Chavez 1983) have shown El Niños to have dramatic impacts on population abundance for some species. Future work testing this idea with scyphomedusae would certainly be interesting. One might develop some index of C. *fuscescens* abundance, monitor the abundance during an extended period of study, then attempt to find some correlation to the cycle of El Niños, rainfall, temperature, etc..

The distribution of scyphistomae in Yaquina Bay appears to be

a function of the availability of suitable substrate. All scyphistomae found were attached to substrate provided by man (rocks comprising jetties and breakwaters, docks, and garbage). This suggests that perhaps jellyfish infestations may not have been common here or elsewhere prior to the construction of jetties, breakwaters and revetments. Here jellyfish infestations are a nuisance to fisherman, and may effect survival of some larval fish stocks (Möller 1980, 1984; Arai & Hay 1982, Bailey & Batty 1983, 1984; Shushkina & Musayeva 1983), and elsewhere such infestations can have a significant economic impact (Cargo & King 1990). If scyphistomae of noxious species exist in similar habitats in other areas perhaps some relief from infestations may be realized by changes in construction methods or remedial actions. At the very least, this distant, pelagic impact of such construction should be considered prior to permitting new work.

Lab Work

No encystment of any scyphistomae was seen during the course of this work. Some polyps died (presumably starved) with no indication of encystment. In one tank a large number of polyps eventually died, the polyps first becoming somewhat amorphous,

coating portions of their rock substrate with a pink film that was still able to capture Artemia nauplii utilizing nematocysts. Finally the slime-like coating disappeared altogether, presumably a result of bacterial degradation.

The planktonkreisel functioned well during the course of this work and the ephyrae it contained achieved growth rates nearly identical to those in the literature for laboratory-reared Chrysaora. Cargo & Schultz (1967) observed growth rates of 0.2mm diameter per day with C. quinquecirrha in the lab feeding strained ctenophores. In the planktonkreisel I observed growth rates of about 0.2mm/day. This is much slower than rates of growth in the field. Shenker (1984) found that mean bell diameter increased from 8.6cm to 18.5cm from May 1981 to August, 1981 for C. fuscescens off Oregon, suggesting an average growth rate of about 1.1mm/day. The largest specimens Shenker collected during this period ranged from 19cm in May to 37cm in August, suggesting a maximum growth rate of about 2mm/day. Cargo and Schultz (1967) calculated rates as high as 5.1mm/day for C. quinquecirrha in the wild. The differences in quality and quantity of available food is likely the reason for the difference between laboratory and in situ growth rates. Aquarist David Compton of the Oregon Coast Aquarium showed me two jellyfish holding tanks containing Aurelia. In the first tank there

were several medusae approximately 2cm across and about 6 months old. In the second tank were more *Aurelia*, these easily twice as large as those in the first tank, but only one month old. According to David Compton, the only difference in rearing between the two was that the second group was fed much more *Artemia* than the first.

The failure of potassium iodide to induce strobilation was surprising, considering the ease in which Spangenberg (1967) was able to initiate it. In this study water temperatures were considerably lower than in Spangenberg's work with Gulf of Mexico Aurelia (14°C vice 27°C, with preconditioning at 8°C vice 19°C), hence one would expect a slower onset of strobilation initiation. Indeed Spangenberg (1967) found 19°C polyps metamorphosed more slowly than 27°C polyps. But here I failed to get any metamorphosis at all after a month using 1:107 and 1:106 dilutions of KI. Spangenberg saw high percentages of the polyps strobilate within two weeks in both temperature ranges she considered, albeit with somewhat lower percentages and longer times at 19°C. More work comparing conditions and dosages will be required to evaluate the potential of iodide treatment for inducing strobilation in Oregon Aurelia.

VI. CONCLUSIONS

My attempt to study *Chrysaora fuscescens* yielded mixed results. Few medusae were encountered during the course of my work and the benthic scyphistoma of *C. fuscescens* life cycle proved elusive. Regional weather conditions, possibly related to the 1993 El Niño event, may have been responsible for the year's low abundance of medusae. I did find scyphozoan polyps in Yaquina Bay, determined during this study to be *Aurelia*, and was able to begin to elucidate their distribution in the bay. The exact location and distribution of *C. fuscescens* awaits future workers. Searches similar to that done here in other estuaries and nearshore regions of our coast may prove fruitful. As in this study, nematocyst typing and laboratory rearing will likely be required for positive identification of newly found polyps.

Found only in the lower part of Yaquina Bay, the distribution of *Aurelia* polyps appears to be determined by the presence of suitable substrate. Substrate provided by human activities, primarily jetties and breakwaters, is likely the primary habitat for the polyps today. Hence such projects may be directly responsible for increases in jellyfish numbers and may be indirectly responsible for increased mortality among larval fishes by increasing predation by jellyfish.

Laboratory culture of the scyphistomae proved successful, allowing positive identification of the scyphistomae found. I reared the jellyfish through their various life stages, scyphistomae through medusae, obtaining growth rates comparable to those found in the literature for laboratory-reared *Chrysaora* -- approximately 0.2mm increase in bell diameter per day -- but well below rates reported from the field. Attempts to induce strobilation utilizing a technique, iodine induction, reported to be quite successful elsewhere proved unsuccessful here, suggesting interesting intraspecific differences in strobilation initiation in *Aurelia*.

BIBLIOGRAPHY

- Arai, M. N. & Hay, D. E. 1982 Predation by medusae on Pacific herring (Clupea harangus pallasi) larvae. Can. J. Fish. Aquat. Sciences 3 9, 1537-1540
- Arai, M. N. & Jacobs, D. R. 1980 Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence. *Can. J. Fish. Aquat. Sciences* 3, 120-123
- Bailey, K. M. & Batty, R. S. 1983 A laboratory study of predation by Aurelia aurita on larvae of flounder, cod, plaice and herring (Clupea harangus): development and vulnerability to capture. Mar. Biol. 8 3, 278-291
- Barber, R. T. & Chavez, F. P. 1983 Biological consequences of El Niño. Science 2 2 2, 1203-1210
- Calder, D. R. 1971 Nematocysts of polyps of Aurelia, Chrysaora, and Cyanea, and their utility in identification. Trans. Amer. Micros. Soc., 9 0(3), 269-274
- Calder, D. R. 1972 Development of the sea nettle Chrysaora quinquecirrha (Scyphozoa, Semaeostomeae). Chesapeake Science 13, 40-44
- Calder, D. R. 1977 Nematocysts of the ephyra stages of Aurelia, Chrysaora, Cyanea, and Rhopilema (Cnidaria, Scyphozoa). Trans. Amer. Micros. Soc., 9 6(1), 13-19
- Cargo, D. G 1972 Comments on the laboratory culture of scyphozoa. Proceedings from the Conference on Culture of Marine Invertebrate Animals, Greenport, N.Y., 1972. Plenum Press, New York
- Cargo, D. G. & King D. R. 1990 Forecasting the abundance of the sea nettle, *Chrysaora quinquecirrha*, in Chesapeake Bay. Estuaries 13(4), 486-491

- Cargo, D. G. & Shultz, L. P. 1966 Notes on the biology of the sea nettle, *Chrysaora quinquecirrha*, in Chesapeake Bay. *Chesapeake Science* 7 (2), 95-100
- Cargo, D. G. & Shultz, L. P. 1967 Further notes on the biology of the sea nettle and jellyfishes in Chesapeake Bay. Chesapeake Science 8(4), 209-220
- Feigenbaum, D. & Kelly, M. 1984 Changes in the lower Chesapeake Bay food chain in the presence of the sea nettle, *Chrysaora quinquecirrha* (Scyphomedusae). *Mar. Ecol. Prog. Ser.* **1 9**, 39-47
- Fofonoff, N. P. & Millard, R. C. 1983 Algorithms for computation of fundamental properties of seawater. Unesco Tech. Pap. in Mar. Sci., No. 44
- Harbison, G. R., Biggs, D. C. & Madin, L. P. 1977 The associations of amphipoda hyperiidea with gelatinous zooplankton--II.
 Associations with cnidaria, ctenophora and radiolaria. *Deep-Sea Research* 24, 465-488
- Hamner, W. M. 1975 Underwater observations of blue-water plankton: logistics, techniques, and safety procedures for divers at sea. *Limnology and Oceanography* **20**(6), 1045-1051
- Hamner, W. M. 1990 Design developments in the planktonkreisel, a plankton aquarium for ships at sea. *Journal of Plankton Research* 1 2(2), 397-402
- Hamner, W. M., Madin, L. P., Alldredge, A. L., Gilmer, R. W. & Hamner, P.
 P. 1975 Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. *Limnology and Oceanography* 2 0(6), 907-919
- Heine, J. H. 1985 Blue water diving guidelines, edited byJ. H. Heine, California Sea Grant College Program Publication No. T-CSGPC-014.

- Huntley, M. E. & Hobson, L. A. 1978 Medusa predation and plankton dynamics in a temperate fjord, British Columbia. J. Fish. Res. Bd. Can. 3 5, 257-261
- Larson, R. J. 1976 Marine flora and fauna of the northeastern United States. Cnidaria: Scyphozoa. NOAA Technical Report NMFS Circular 397
- Larson, R. J. 1986 The feeding and growth of the sea nettle, *Chrysaora quinquecirrha* (Desor), in the laboratory. *Estuaries* 9(4B), 376-379
- Larson, R. J. 1990 Scyphomedusae and Cubomedusae from the eastern Pacific. *Bulletin of Marine Science* **4** 7(2), 546-556
- Laval, P. 1980 Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. Oceanography and Marine Biology Annual Review 18,11-56
- Mansueti, R. J. 1963 Symbiotic behavior between small fishes and jellyfish with new data on that between the stromeid, *Peprilus alepidotis*, and the scyphomedusa, *Chrysaora quinquecirrha*. *Copia* 1963(1), 40-80
- Miller, C, B. 1983 The zooplankton of estuaries. Estuaries and Enclosed Seas, edited by B. H. Ketchum. Elsevier Scientific Publishing Company, Amsterdam.
- Möller, H. 1978 Significance of coelenterates in relation to other planktonic organisms. *Meeresforschung* 27, 1-18
- Möller, H. 1980 A summer survey large zooplankton, particularly scyphomedusae, in North Sea and Baltic. *Meeresforschung* 28, 61-68
- Möller, H. 1984 Reduction of larval herring population by jellyfish predator. Science 209, 1045-1047

- Russell, F. S. 1970 The medusae of the British Isles. II. Pelagic Scyphozoa, with a supplement to the first volume of Hydromedusae. Cambridge Univ. Press, Cambridge. 284 p.
- Shenker, J. M. 1984 Scyphomedusae in surface waters near the Oregon Coast, May-August, 1981. Estuarine, Coastal and Shelf Science 19, 619-632
- Shenker, J. M. 1985 Carbon content of the neritic scyphomedusae Chrysaora fuscescens. Journal of Plankton Research 7(2), 169-173
- Shushkina, E. A. & Musayeva, E.I. 1983 The role of jellyfish in the energy system of Black Sea plankton communities. *Oceanology* 2 3, 92-96
- Sommer, F. A. 1992 Husbandry aspects of a jellyfish exhibit at the Monterey Bay Aquarium. American Association of Zoological Parks and Aquariums Regional Conference Proceedings
- Spangenberg, D. B. 1967 lodine induction of metamorphosis in *Aurelia. J. Exp. Zool.*, **165**, 441-450
- Spotte, S. 1979a Fish and invertebrate culture: Water management in closed systems, 2nd edition. Wiley-Interscience, New York. 179 p.
- Spotte, S. 1979b Seawater aquariums: The captive environment. Wiley-Interscience, New York.145 p.
- Strand, S. W. & Hamner, W. M. 1988 Predatory behavior of Phacellophora camtschatica and size-selective predation upon Aurelia aurita in Saanich Inlet, British Columbia. Mar. Biol. 99, 409-414
- Strathmann, M. F. 1987 Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Seattle. 670 p.