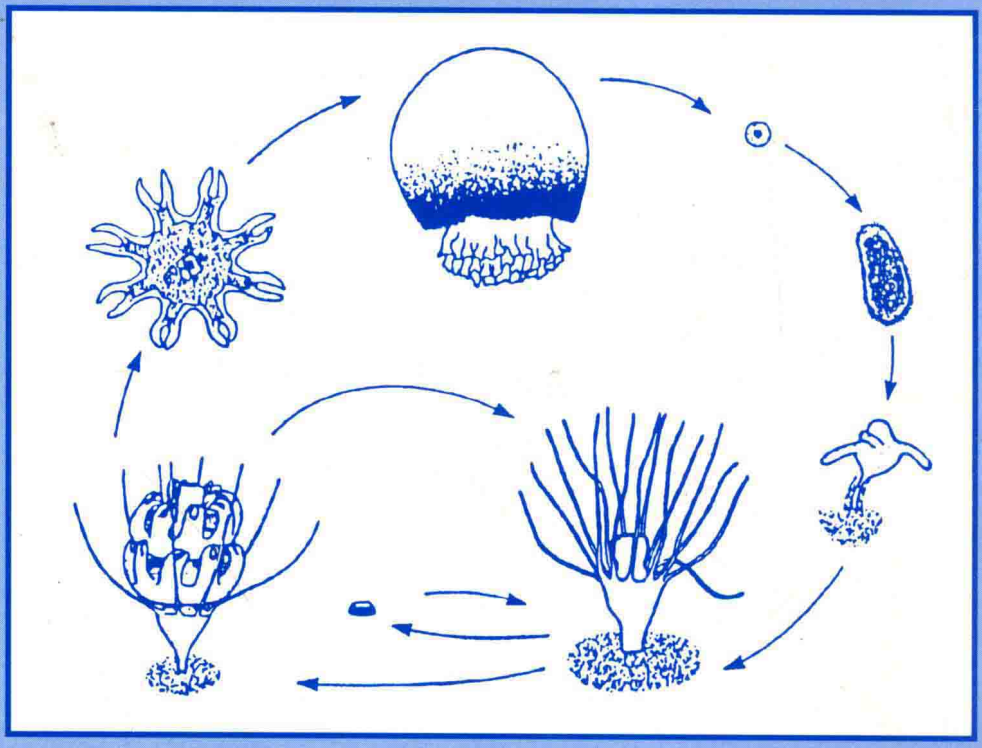
Mary N. Arai

A Functional Biology of Scyphozoa



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A Functional Biology of Scyphozoa

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To my family, past and present

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Preface

Scyphozoa have attracted the attention of many types of people. Naturalists watch their graceful locomotion. Fishermen may dread the swarms which can prevent fishing or eat larval fish. Bathers retreat from the water if they are stung. People from some Asiatic countries eat the medusae. Comparative physiologists examine them as possibly simple models for the functioning of various systems. This book integrates data from those and other investigations into a functional biology of scyphozoa. It will emphasize the wide range of adaptive responses possible in these morphologically relatively simple animals.

The book will concentrate on the research of the last 35 years, partly because there has been a rapid expansion of knowledge during that period, and partly because much of the previous work was summarized by books published between 1961 and 1970.

Bibliographies of papers on scyphozoa were included in Mayer (1910) and Kramp (1961). Taxonomic diagnoses are also included in those monographs, as well as in a monograph on the scyphomedusae of the USSR published by Naumov (Naumov, 1961). Most importantly, a generation of scyphozoan workers has used as its 'bible' the monograph by F.S. Russell (1970) *The Medusae of the British Isles*. In spite of its restrictive title, his book reviews most of the information on the biology of scyphozoa up to that date.

The expansion of knowledge since 1970 has not been even. It has been especially driven by the instances in which scyphozoa have impinged on human activities. We know more about the effects of cnidae on humans than on natural prey. There have been a number of studies on the effects of scyphozoa on fisheries, but we know very

little about predation on scyphozoa. A great deal of new information on *Pelagia noctiluca* was generated because a 'bloom' in the Mediterranean Sea in the early 1980s affected tourism.

In other cases, however, the emphasis has indeed been on how a relatively simple animal is able to carry out its functions. The ways in which a simple nerve system transmits information have been examined, with particular reference to the properties of the bidirectional synapses in the nerve net. The ability of medusae to migrate horizontally using information from the sun has been established, although we do not yet understand the mechanisms. In this book I will pull together the diffuse literature, and give as balanced a view as possible of the biology of the group.

With the emphasis on functional biology, neither taxonomy nor morphology are extensively dealt with. However, Chapter 1 briefly introduces the design of each of the orders, and the Appendix lists by family those species that are mentioned in the text. Morphological structures are described in the context of their functions.

Terminology has been kept as simple as possible and is defined as it arises. Definitions are indicated in bold type in the index. Where greater detail on these subjects is desired the reader is referred to Russell (Russell, 1970), and to the review by Franc in the Traité de Zoologie (Franc, A., 1993).

Mary Needler Arai
Calgary
May 1996

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1 *Design and relationships*

1.1 INTRODUCTION

The Scyphozoa constitute one of the four classes of living cnidaria. The members of the phylum Cnidaria are characterized by the possession of intrinsic cnidae: intracellular organelles consisting of a capsule and an attached hollow thread. Cnidarian animals consist of two epithelial body layers, the epidermis and gastrodermis, separated by a gelatinous connective tissue, the mesoglea. These three layers form a sac around the gastrovascular cavity or coelenteron which usually has a single opening, the mouth. Typically tentacles form a ring around the margin of an oral disc surrounding the mouth.

Cnidarians exhibit two adult body forms. One form, the medusa or jellyfish, is typically solitary, pelagic, with two saucer shapes of the three layers fused at the margins to form a bell with the mouth on the undersurface (subumbrella). The mesoglea is relatively thick. The other form, the polyp, is solitary or colonial, typically attached to a substrate with the mouth upwards. The mesoglea is relatively thin.

Other possible life history stages include a simple larva, the planula, and buds and cysts. The typical cnidarian life cycle includes a planula which develops into a polyp, which in turn asexually produces medusae which reproduce sexually (Figures 1.1, 6.1, 6.6). However, any of these stages can be reduced or absent, cysts may be included, and polyps may give rise asexually to more polyps (Figure 1.2) or may be the stage that reproduces sexually.

Fundamentally, scyphozoa are tetraradially symmetrical having many structures in multiples of four. Most medusae of the Scyphozoa

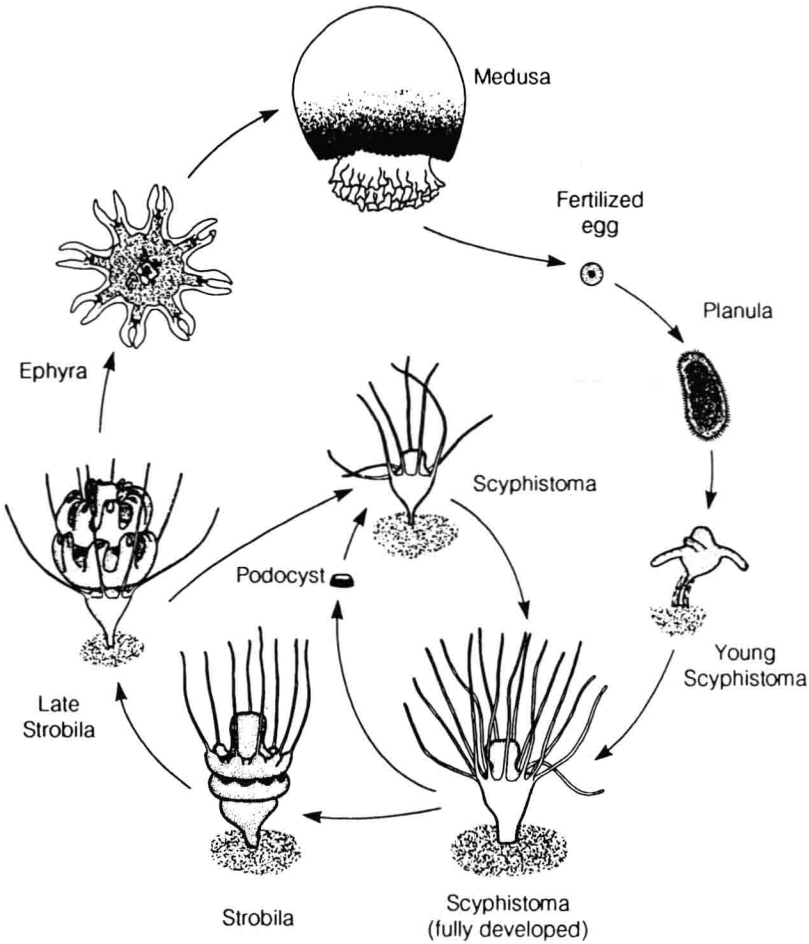

Figure 1.1 Life cycle of the rhizostome scyphozoan *Stomolophus meleagris*. The fertilized egg develops into a cilated planula larva which settles and forms a polyp, the scyphistoma. The scyphistoma can reproduce asexually either via a cyst, the podocyst, to form more scyphistomae, or by strobilation to form ephyrae which develop into medusae and reproduce sexually. (Source: Calder, 1982, with permission of D.R. Calder and *Biological Bulletin*.)

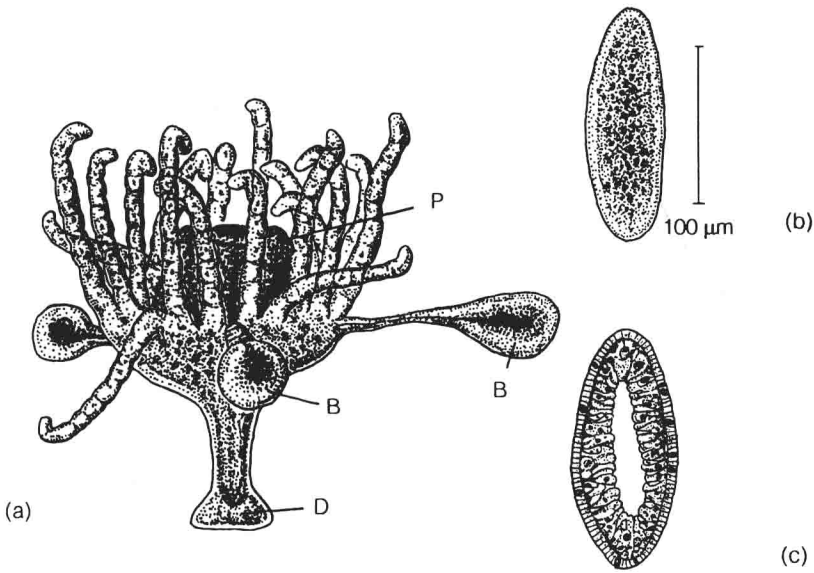

Figure 1.2 The interstitial scyphozoan *Stylocoronella riedli*. In asexual reproduction the polyp sheds buds which form unciliated planuloids and grow into new polyps. (a) Polyp; (b) free planuloid; (c) longitudinal section through a planuloid. B = bud; D = pedal disc; P = proboscis with mouth. (Redrawn from Salvini-Plawen, 1966, with permission of L. Salvini-Plawen.)

differ from those in the Cubozoa and Hydrozoa in lacking any shelf of tissue (velum or velarium) extending inward from the margin into the subumbrellar space. Scyphozoa lack a clearly defined pharynx leading in from the mouth such as is present in the Anthozoa. In Scyphozoa and Cubozoa there are gastric cirri in the stomach. The mesoglea maybe cellular and the gonads are gastrodermal in origin.

Scyphozoa are exclusively marine. Their medusae are found in pelagic habitats from the surface to very deep water. Their polyps are found attached to a wide variety of substrates. The only interstitial genus, *Stylocoronella*, includes two species of minute immature stauromedusan polyps, *S. riedli* and *S. variabilis* (see Salvini-Plawen, 1966, 1987; Kikinger and Salvini-Plawen, 1995) (Figure 1.2).

1.2 THE ORDERS: MORPHOLOGY AND LIFE CYCLES

In the Scyphozoa the medusoid stage typically predominates whereas the polypoid stage is very small. In many species the polyp is unknown,