

THREE

Phylum CTENOPHORA

comb jellies

HERMES MIANZAN, ELLIOT W. DAWSON, CLAUDIA E. MILLS

Ctenophores have been described as the most beautiful, delicate, seemingly innocent yet most voracious, sinister and destructive of plankton organisms. They are exclusively marine, are found in all oceans at all depths, have many different shapes, and range in size from a few millimetres diameter to two metres long. They are mostly planktonic, but one order is bottom-dwelling with a creeping mode of existence. The planktonic forms are stunningly beautiful, diaphanous creatures, flashing iridescence as their comb-like cilia plates catch the light. Their bodies are soft, fragile, gelatinous. The phylum is small and well defined, with about 150 species worldwide (Mills 2008). Like the Cnidaria, they are radiate animals and at one time the two phyla were linked together as the Coelenterata. Ctenophoran symmetry is biradial and the general body plan somewhat more complicated than that of Cnidaria (Harbison & Madin 1982; Mills & Miller 1984; Harbison 1985). The two phyla are now thought to be only very distantly related. Recent evidence from ribosomal RNA sequencing shows that the Ctenophora lie close to the Porifera as the second-most-basic group of the Metazoa (Bridge et al. 1995; Collins 1998; Podar et al. 2001). Similarity in body form between pelagic ctenophores and medusae is a phenomenon of convergence.

Ctenophores (literally, comb bearers) are named for their eight symmetrical tracks (comb rows) of fused ciliary plates (ctenes) on the body surface (Hernández-Nicaise & Franc 1993). These constitute the locomotory apparatus that characterises the group. Ctenophores are, in fact, the largest animals that use cilia for locomotion. Metachronal beating of the ctenes produces swimming in all but the adult creeping forms and is co-ordinated by an apical sense organ, the statocyst. Tentacles, when present, usually bear adhesive cells called colloblasts, another unique feature of the phylum, which serve to capture prey. Ctenophores are not only iridescent; bioluminescence is a common feature in most species (Haddock & Case 1995) and, in some, clouds of a bioluminescent substance are expelled, probably as a means to avoid predation (Harbison 1996).

The digestive or gastrovascular system can be divided into an axial portion – consisting of a large stomodeum (pharynx), infundibulum (gut), infundibular canal, anal canals, and pores – and a peripheral portion – consisting of perradial, interradial, adradial and meridional canals, tentacular canals, and paragastric canals. Any of them may be missing, except for the adradial and meridional canals (Harbison 1985). Most ctenophores are simultaneous hermaphrodites, capable of self-fertilisation. Only the genus *Ocyropsis* has been reported as dioecious (Harbison & Miller 1986). The Platyctenidae, as an exception to the rule, is protandrous, and asexual reproduction has also been recorded (Harbison 1985).

As soft-bodied organisms, ctenophores are rarely preserved as fossils (cf. Conway Morris & Collins 1996), so their phylogenetic relationships are still not well understood. Traditionally, the phylum comprises two classes – Nuda and Tentaculata. The Nuda includes just one order, Beroida, whose species lack



Leucothea sp.
Darryl Torckler

tentacles during their entire life. The Tentaculata includes eight orders (Mills 2008). The species of Cydippida, thought to be the most primitive order, retain their tentacles throughout life. The order Platyctenida is a benthic group that lost the ctenes as an adaptation to the benthic lifestyle of the adult. The orders Cambojiida and Cryptobiferida are mono- or bigeneric, proposed by Ospovat (1985) for forms that are substantially different from other orders. The orders Thalassocalycida and Ganeshida are monogeneric and were proposed for forms that did not fit the definitions of the other orders (Harbison 1985). The order Lobata is easily recognisable by the presence of large oral lobes and auricles, and by the absence of tentacular sheaths. The order Cestida has members with a ribbon-like body and modified tentacles that run along its length.

Harbison et al. (1978) summarised present knowledge of the phylum, the classification of which is in continuous change as more is learned (Harbison & Madin 1982; Ospovat 1985; Harbison 1985, 1996; Mills 2003). Current taxonomy of the Ctenophora is very complex indeed. The list of known species is continuously expanding because new species and genera have yet to be described. Using a submarine, in one single cruise Harbison (1986) found over 22 mesopelagic species of which only five had been described previously. In contrast, at least 50 species have been assigned to the genus *Beroe*, but many of them are unresolved synonyms (Tiffon 1993; Mills 2008). The genus *Euplokamis* has similarly been revised based on its unusually complex tentacles (Mills 1987), each provided with a giant nerve axon (Mackie et al. 1988). The higher taxa are greatly in need of revision. A new classification was developed on the basis of the ctenophore peristomial system, adding two new subclasses (Ospovat 1985), but it has not been followed in later taxonomic papers. The diagnostic characters may be inadequate, as some of the new findings have been ascribed to new structural levels (families and orders); this is demonstrated by the high percentage of monogeneric orders.

Distribution of ctenophores

Major works on ctenophore taxonomy have usually focused on restricted geographic areas. For example, Chun (1880) described ctenophores from the Gulf of Naples, Italy. Mayer (1912) presented an important contribution for northwestern Atlantic waters, and Bigelow (1912) covered the eastern tropical Pacific. Moser (1910) produced the first worldwide distributional study, but the southern oceans remained with only a few species-specific records. Recently, Hernández-Nicaise and Franc (1993) published an updated geographic distribution of the Ctenophora, and it is clear that a very noticeable gap still remains in the southern oceans, although Mianzan (1999) has updated information from the South Atlantic. Wrobel and Mills (1998, 2003) and Mills and Haddock (2007) provided information on ctenophores in the northeast Pacific, including some deep-water species.

Ecology

All ctenophores are carnivorous, feeding on zooplankton of various sizes, including copepods, amphipods, euphausiids, appendicularians, fish eggs, and larvae. Some, like the Beroida, feed on gelatinous plankton such as other ctenophores, medusae, and salps (Fraser 1962, 1970; Swanberg 1974; Kremer 1979; Mianzan & Sabatini 1985; Purcell 1985; Monteleone & Duguay 1988; Mills unpubl.). Their role in marine food webs is more complex than previously thought. Ctenophores were long considered a trophic dead-end in marine food webs, but recent studies indicate that they may be consumed by various fish species (Oviatt & Kremer 1977; Arai 1988; Ates 1988), following a seasonal pattern (Mianzan et al. 1996). More complex trophic relationships also imply an active role in the transmission of parasites – the first record of a metacercarian flatworm encysted in ctenophores in southern waters was recently published (Martorelli 1996; cf. also Boyle 1966).

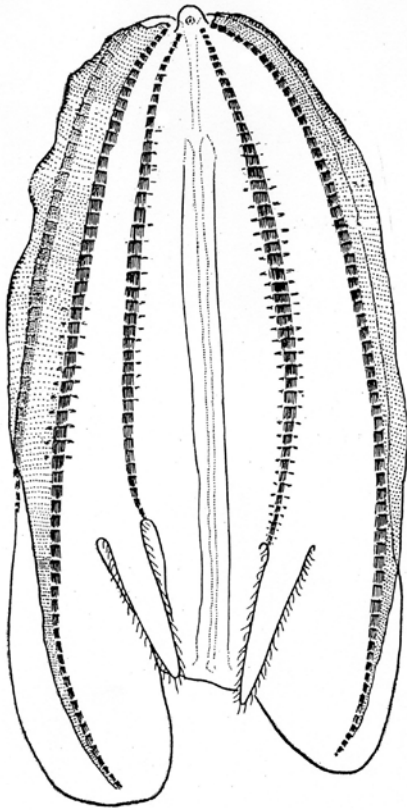
Invasive species

It is well known that ctenophores occur from time to time in vast numbers in coastal and estuarine regions of the world's oceans (Fraser 1962; Hirota 1974; Harbison et al. 1978). A number of authors have concluded that coastal species are important predators that can regulate the abundance of certain herbivores (Harbison et al. 1978; Deason 1982; Feigenbaum & Kelly 1984; Mianzan & Sabatini 1985). Recently, apparently transported in ballast water, an immigrant species of the New World genus *Mnemiopsis* has invaded the Black Sea, leading to the collapse of local pelagic fisheries (Shushkina & Musayeva 1990; Vinogradov et al. 1989; Zaika & Sergeyeva 1990; for reviews see GESAMP 1997 or Shiganova 1998). Losses are estimated at more than US \$200 million. Members of this genus are hermaphroditic, capable of self-fertilisation, and can release more than 10,000 eggs over their lifetimes (Reeve et al. 1989). In the past decade, *Mnemiopsis leidyi* has further spread to the Caspian Sea, eastern and western Mediterranean, and most recently to the North and Baltic Seas (Javidpour et al. 2006; Oliveira 2007). Its tolerance to a wide range of salinities is incredible – it can survive between 5 and 70 practical salinity units. With such capabilities, it is easy to understand how *M. leidyi* could survive ballast transport and quickly take advantage of the resources of a particular ecosystem (cf. Lynch 1997). Ironically, the solution to the problem now appears to be a species of *Beroe*, a ctenophore predator of ctenophores and other gelatinous organisms. Lacking tentacles, *Beroe* feeds in a different manner and on different prey than does *Mnemiopsis*.

History of studies on New Zealand Ctenophora

Historically, the first ctenophores to be observed in New Zealand waters were mentioned by Sydney Parkinson, one of Banks's two botanical artists on Cook's first voyage. He recorded '*Beroe coarctata*' seen on 5 October 1769 shortly before the *Endeavour* reached the east coast of the North Island (Parkinson 1773, pp. 86, 87). Andrews (1986, p. 4, note 20) stated that a '*Beroe* was described by Solander on 6 October, Sol. MS Z4, Zoology Library, British Museum (Natural History)'. Beaglehole (1962, p. 396) noted that Joseph Banks had collected *Beroe incrassata* and *B. coarctata*, 'with several other things which are all put in spirits', on 2 October 1769, and, referring to the drawing by Parkinson and the description by Solander, suggested in a footnote that *Beroe incrassata* is 'probably' *Beroe ovata* and that *B. coarctata* is 'possibly' a species of *Lampetia* (now *Lampea*).

According to Benham (1907, p. 139), the only ctenophore attributed to New Zealand seas prior to his own review was a pleurobrachiid named *Cydidippe dimidiata* Lesson, collected in the Tasman Sea in 1770 by Banks and Solander during Cook's first voyage and originally named by them *Beroe biloba*, subsequently placed by Lesson in his genus *Eschscholthia*. In the first complete checklist of the New Zealand fauna, Hutton (1904, p. 314) listed it as *E. dimidiata* Lesson. Benham, however, concluded: 'It has not been studied further, and nothing more is known of it other than the short account given by Lesson. I think that it may well be removed from our list.' We chose to retain it in the present species list for full historic perspective. Benham (1907) made the first local study of the New Zealand Ctenophora by describing two new species – *Beroe shakespearei* (= *B. ovata*, *fide* Mills 2008 following Bigelow 1912), from off Little Barrier Island (Hauraki Gulf), D'Urville Island (Cook Strait), and Tauranga (Bay of Plenty), and *Euplokamis australis* (now in *Pleurobrachia*) (Mills 1987, 2008) from a single individual off Farewell Spit (Cook Strait), several juveniles from Otago Harbour, and one from Port Jackson. In 1904, the Italian naval vessel *Liguria* took plankton samples in the New Zealand region, and the ctenophores collected were described by Ghigi (1909). These were *Hormiphora labialis* n. sp., based on a single specimen taken at *Liguria* Station XX, northeast of Norfolk Island (Australian EEZ), 18 July 1904, and *Sabaudia liguriae* n. gen., n. sp., based on four specimens taken at *Liguria* Station XXI northeast of Banks Peninsula,



Lesueuria pinnata, a bolinopsid lobate ctenophore from Cook Strait.
From Ralph & Kaberry 1950

29 July 1904. Soon after, Moser (1909) listed Hamburg Museum specimens of *Pleurobrachia pileus* (Müller), collected at Tauranga by Thilenius, as *P. bachei* A. Agassiz. Next, Benham (1910) drew local attention to Ghigi's paper (which is still not well known).

Kaberry (1935) made the first contribution to our knowledge of the identity and ecology of ctenophores at a particular geographic locality in New Zealand. His unpublished thesis resulted from a year-long study (July 1934 to July 1935) of the pelagic coelenterates of Cook Strait, offshore of Island Bay on the exposed Wellington south coast. This particular season, he noted, was one of the 'quietest and hottest experienced for many years, and with an absence of wind has been very important in the collection of delicate forms'. He included an account of the ctenophores he found: *Pleurobrachia pileus*; *P. brunnea* (?), *Euplokamis australis* (?), *Lesueuria* (?) sp., and *Bolinopsis* sp. (?) (see below); *Leucothea multicornis*; *Ocyropsis crystallina* (?); *Cestum veneris*; and *Beroe shakespearei* (?). Kaberry wrote vividly of his difficulties in collecting ctenophores from his 2.7-metre boat, laboriously rowing several kilometres offshore, then transporting them eight kilometres back to the laboratory, travelling on a motor cycle, and discovering that a speed of 50–70 kilometres per hour was least damaging! Listing a series of chemical methods for their preservation he had tried, Kaberry concluded that *Pleurobrachia pileus* and the species of *Beroe* stored well in formalin, whereas *Bolinopsis*, *Cestum veneris*, *Leucothea multicornis*, and *Ocyropsis crystallina* proved to be absolutely soluble in formalin, leaving only a few ctene plates in the bottom of the jar, hence the difficulty now of being able to verify his record of the last-named species.

Ralph (1950) also reported on collections from Wellington environs. These included: *Beroe forskalii* from Princess Bay on the south coast, 1945; *B. cucumis*, taken off Island Bay in 1935 by Kaberry; juvenile *Beroe* from a tow off Barrett Reef at the entrance to Wellington Harbour in 1947; and *Pleurobrachia pileus* off Barrett Reef and Point Halswell, January 1947 to February 1948. Juveniles attributed to *Lampetia* collected by Kaberry off Island Bay in October 1942 were also noted. Ralph and Kaberry (1950) continued work on the Cook Strait ctenophores by describing and figuring three new species, all collected by Kaberry during 1934 and 1935: *Pleurobrachia helicoides* ('*Pleurobrachia brunnea* Mayer, 1912 (?)' of Kaberry 1935), from two collections, 22 and 23 July 1935; *Bolinopsis paragaster* ('*Bolinopsis* sp. (?)' of Kaberry 1935), collected in late autumn (March and April) 'when they often formed a major part of the pelagic fauna'; *Lesueuria pinnata* ('*Lesueuria* (?) sp. cf. *L. hyoptera* A. Agassiz, 1865' of Kaberry 1935), noted as 'common during calm weather in autumn but is very difficult to capture on account of its size and delicate nature, while an hour or so of confinement is sufficient to start disintegration'. They also observed *Pleurobrachia pileus* as an efficient fish catcher and highlighted the difficulties of working with ctenophores using the example of *Leucothea multicornis*: 'This species observed in autumn during very calm weather was one of the most delicate ctenophores taken, and extremely difficult to handle,

Summary of New Zealand ctenophoran diversity

Taxon	Described species	Known undescribed/undetermined species	Estimated unknown species	Endemic species	Endemic genera
Tentaculata	12	4	10	5?	0
Cydippida	5	2	5	3?	0
Platyctenida	1	0	0	0	0
Lobata	4	2	5	2?	0
Cestida	2	0	0	0	0
Nuda	3	0	2	0	0
Beroida	3	0	2	0	0
Totals	15	4	12	5?	0

as it extruded great quantities of slime when captured. Any slight movement of the boat always tore the specimens to pieces so that only fragments ever reached the laboratory.' *Cestum veneris* was collected on five occasions during prolonged calm weather in March and in May when this species was 'plentiful, almost sufficient to be called a swarm.' Boyle (1966) later described parasitic trematodes and nematodes from *Pleurobrachia pileus* collected in the area.

The only new identifications of ctenophores in the New Zealand region since have been Gordon's (1969) record (and southernmost known occurrence) of the platyctenean *Coeloplana willeyi*, cast ashore on Pakiri Beach, Northland, on a colony of the bryozoan *Diaperoecia purpurascens* (as *Entalophora*), and subsequently found nearby off Goat Island. Later, Gordon and Ballantine (1977) listed *Velamen* (?) sp. and *Bolinopsis* sp. from the outer gulf waters off Leigh. The former record has been confirmed as monospecific *Velamen parallelum* by Dr S. Cook (pers. comm.), who noted these slender, darting cestids when diving near Goat Island. *Pleurobrachia pileus* and *Beroe* sp. were taken regularly in plankton hauls off Menzies Bay, Banks Peninsula, in May during the Canterbury University student field trips traditionally held there by Professor E. Percival.

C. E. Mills carried out field work on gelatinous plankton at marine laboratories in New Zealand from 27 October 1981 to 9 January 1982, and previously unpublished observations (see page 56) of the ctenophores encountered include:

- *Pleurobrachia pileus* (?): many, Leigh, Northland, 28 October 1981; many, Whangateau Harbour, Northland, 4 November 1981; many, off Orakei Bridge and Westhaven Marina, Auckland, 10 November 1981; many at the surface, Goat Island Bay, Northland, 11–12 November 1981 and collected by B. Thompson on 22 and 25 November 1981; many off tip of Kaikoura Peninsula, 23 December 1981.
- *Hormiphora* sp.: 24 December 1981 (also in preserved samples at Portobello Marine Laboratory: [1] collected by D. Robertson, 30 January/4 February 1972, off Kaikoura beyond the 500 m isobath; [2, 3] hundreds washed up on the sand at Little Papanui Beach, 18 December 1957 and 29 March 1963).
- *Bolinopsis* sp.: few at the surface, Kaikoura, 24 December 1981.
- *Pleurobrachia* sp. or *Hormiphora* sp.: preserved, a few taken in a plankton sample by B. Thompson on 22 November 1981 at the surface in Goat Island Bay, Northland.
- *Coeloplana willeyi*: many, collected by C. N. Battershill on the sponges *Raspailia topsenti* and *Ancorina alata* in the 'Sponge Gardens', near the Leigh Laboratory, 3 November 1981 and 4 January 1982.

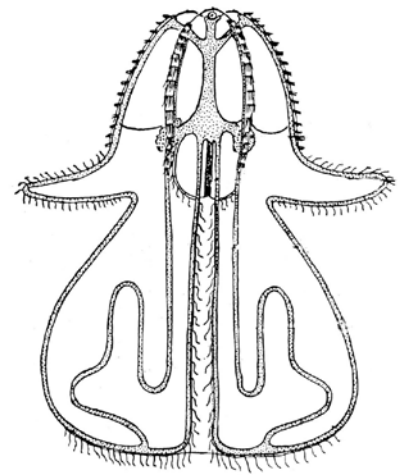
Ctenophora are regularly taken in most planktonic investigations of New Zealand waters; for example, Hauraki Gulf (Cassie 1966; Jillett 1971); Wellington Harbour (Wear 1965); Otago shelf (Jillett 1976); Campbell Island (Roberts 1972). Additionally, some popular accounts of New Zealand marine life or similar texts have mentioned or illustrated ctenophores in passing (e.g., Miller 1965; Natusch 1967; Doak 1971, Westerskov & Probert 1981; Powell 1997 [1947]; Anderson 2007).

Here our knowledge of the New Zealand Ctenophora rests. Nothing is known of their roles in local food webs but, judging from overseas work, they are probably significant predators of ichthyoplankton – a good reason for new studies to be attempted. As with so many other groups, the need for thorough taxonomic work must be emphasised.

The New Zealand ctenophore fauna

Current known diversity

The New Zealand ctenophore fauna (EEZ) currently stands at 19 species, five are which are nominally locally restricted (Dawson 1992; Mills unpubl.), but the true taxonomic composition of the fauna mirrors the situation for the phylum worldwide. There is much uncertainty about the precise identity of many of the



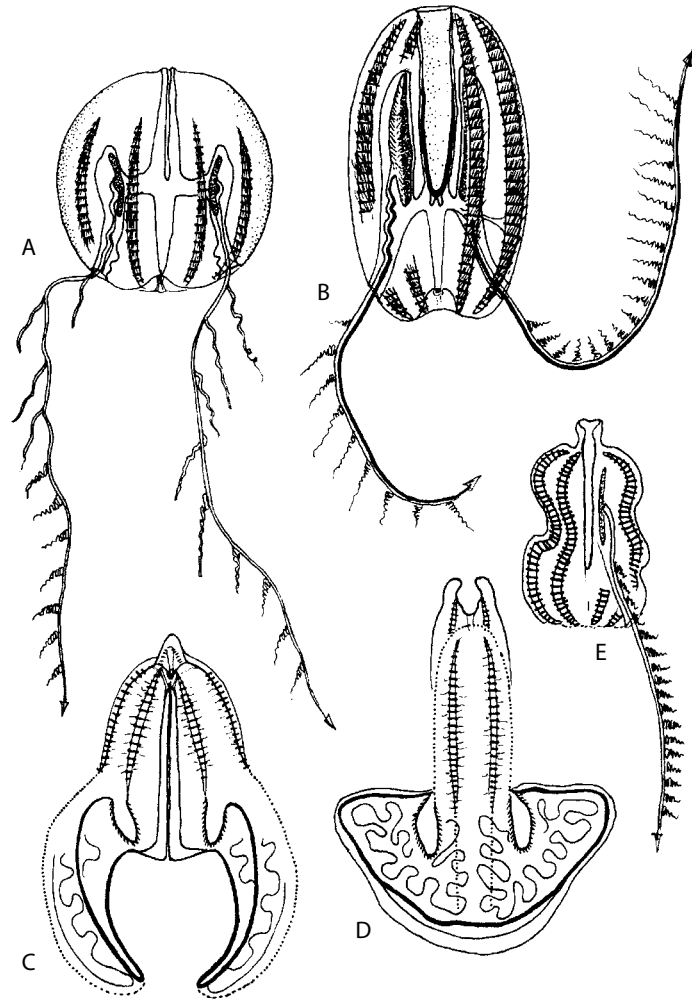
Bathocyroe paragaster, a bathocyroid lobate ctenophore from Cook Strait.

From Ralph & Kaberry 1950

species, some of which are known from only a single specimen, and the range of variation, even in the more abundant and better-known species, is equally uncertain. Before we are able to make statements about the degree of endemism or the unique aspects of the New Zealand ctenophore fauna, we need to have new collections. We also need to examine such specimens as still exist from previous collecting (such as Ghigi's *Liguria* types), especially in the light of later ideas as to what constitutes a species in the Ctenophora. All 19 species are listed in the checklist. Local lists of New Zealand ctenophores (Dawson 1992, 1998, in press) are based on these species names.

How can we increase knowledge of New Zealand ctenophore diversity?

The researcher who wants to undertake a scientific study of ctenophores must be warned that they are among the most difficult marine animals to work with (Harbison 1986). Their fragility renders them notoriously difficult to obtain using conventional sampling methods because they tend to collapse (Harbison et al.



Ctenophores collected by C. E. Mills in New Zealand in 1981.

A: *Pleurobrachia pileus* (?) (to 7 mm diameter, transparent and colourless, comb rows extend half body length in small specimens to three-quarters body length in the largest), from Leigh, Northland. B: *Hormiphora* sp. (20 mm long, comb rows extend entire body length with large, heavy ctenes and with pale lilac pigment, tentacles each with a line of dark reddish-purple pigment opposite the tentillae and pharynx with two, distinctive dark reddish-purple pigment lines that survive preservation), from Kaikoura. C, D: *Bolinopsis* sp. (70 mm long, transparent and colourless except for black pigment line outlining each lobe), from Kaikoura. E: *Pleurobrachia* sp. (?) or *Hormiphora* sp. (?) (10 mm long, colourless), from Goat Island Bay, Northland.

A–D drawn from life; E from preserved specimen

Claudia Mills

1978). Based on the results of quantitative sampling, one gains the impression that ctenophores represent an insignificant fraction of the fauna of the open sea (Harbison 1986), but Hardy (1956) indicated long ago that this might be an illusion. Of those few specimens that can be collected with nets, only a small fraction can be preserved in recognisable condition (Harbison 1986), mainly Cydippida and Beroida. Bathypelagic ctenophores usually do not survive a simple plankton tow, and even the very tough bodies of some coastal Lobata disintegrate immediately after being put into formalin, notwithstanding very low concentrations.

In situ techniques such as diving or use of submersibles have proved to be excellent for collecting these delicate animals alive, although preservation beyond photography remains a problem. Improper fixation produces a mass of amorphous or disintegrated jelly and disarranged or detached comb plates. Some distortion and shrinkage of specimens is to be expected however careful the preparation. Formalin solutions are inadequate to fix most ctenophores. Early methods using solutions containing osmic or chromic acid caused discoloration and sometimes disintegration of the specimens. We recommend the procedures described in Adams et al. (1976) and O'Sullivan (1986) as the most effective found so far for most forms. An especially useful new guide to the gelatinous plankton, which includes methods of collection, observation, and photography, is that of Wrobel and Mills (1998).

Taxonomy

Species identification of ctenophores is difficult. Owing to the problems outlined above, many original descriptions are based on specimens that were distorted or damaged by collection and preservation. Many descriptions are also based on juvenile animals that have not yet been linked to their adult forms. Care must also be taken with juveniles of several species in the class Tentaculata because adults without noticeable tentacles pass through a tentacular stage during development, resembling cydippid larvae, which further confuses proper identification. As a result, attributions of local races or varieties to new species are common in the literature. Five of the species in the checklist have been found only in New Zealand waters, possibly suggesting an important level of endemism but equally indicating the need for more detailed study of their true identity.

Adventive species

There is no information about invasive species in New Zealand waters. Present knowledge of New Zealand ctenophores is insufficient for perceiving biogeographical patterns. This review is the first attempt to assemble all available information about New Zealand Ctenophora.

Gaps in knowledge and scope for future research

The global decline in taxonomic expertise has led to a situation where there are today very few people working on ctenophore systematics. This must be remedied if the role of ctenophores in the economy of the oceans is to be fully appreciated. A complete description of species distribution is still pending. Global knowledge is based on very dispersed collections and isolated references to capture of particular species in specific localities. A new strategic programme of research involving people in many countries needs to be undertaken, focusing on the taxonomy of this group, leading to distributional mapping and subsequent ecological analyses. As described above, the challenges relating to conventional collecting necessitate the use of *in situ* methods of live collecting, macrophotography, genetic comparisons, and improved preservation. Only in this way can an accurate picture be established of distribution and biomass. It is ironic that members of the order Lobata, which achieve enormous biomasses in coastal waters, are so fragile and disintegrate so easily in preservative, confounding an appreciation of the importance of the group. The same constraints apply in

deeper water where ctenophores appear to be significant predators. In New Zealand, all ctenophores are under-sampled, especially lobates, and the group as a whole is very poorly represented in museum collections. Given the large size of the New Zealand EEZ, it is certain that the role of ctenophores in the ocean ecosystem is vastly underestimated. New Zealand should be an active participant in any global programme of research.

Conclusions

Fundamentally, published knowledge of the taxonomic identity and ecology of New Zealand ctenophores relies almost entirely on the work of Kaberry (1935), Ralph (1950), and Ralph and Kaberry (1950) in central New Zealand waters. The records of Gordon and Ballantine (1977) from northern New Zealand suggest the presence there of a different faunal element. Despite their demonstrated intransigence to collecting and preservation, the Ctenophora offer a positive challenge for new students and the agreeable prospect of hand-collection from small boats on fine days or by diving. The offshore waters adjacent to the various marine laboratories, so conveniently latitudinally (and hydrologically) spaced along the coastline of New Zealand – Leigh 36°S, Island Bay 41°S, Kaikoura 42°S, and Portobello 46°S – could provide sound bases for comparative analyses of distribution (including seasonal changes and variation) and ecology. Oceanic species are frequently encountered at the Poor Knights Islands (35°S). Correlations between surface-water movements and seasonal temperature variations (as now regularly mapped from satellite records by NIWA) are known for some marine invertebrates around New Zealand that are relevant to studies of Ctenophora (cf. Jillett 1976; Dawson & Yaldwyn 2000).

We herewith issue a research challenge posed by the New Zealand Ctenophora and share with the reader two quotations – the first of which serves to recall the pioneer work of A. C. Kaberry, without whose dedicated efforts, 65 years ago, knowledge of this phylum would have been so much poorer.

‘Very little has been written about New Zealand sea-gooseberries, but examples are commonly found by towing a muslin net from a small boat’ (Powell 1997, p. 7, first written in the year 1947, and still unchanged).

‘The ctenophores may be counted among the most beautiful and delicate of plankton organisms, yet in truth, in spite of their innocent appearance, they are also to be considered among the most voracious. They sometimes occur in enormous numbers and must then seriously reduce the population of animals upon which they prey, including the fry of many commercial fish as well the small crustaceans upon which so many of our young fish depend for food; it has, I think, only recently been realised what a very important – not to say sinister – part these seemingly fragile creatures play in the general economy of the sea . . . Their power of destruction is not surprising . . .’ (Hardy 1956, pp. 133–134).

Authors

Dr Hermes Mianzan CONICET–Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), PO Box 175, 7600 Mar del Plata, Argentina [hermes@inidep.edu.ar]

Elliot W. Dawson 17 Kotari Road, Days Bay, Eastbourne, Wellington 5013, New Zealand [edawson@xtra.co.nz]

Dr Claudia E. Mills Friday Harbour Laboratories, University of Washington, 620 University Road, Friday Harbour, WA 98250, USA [cemills@u.washington.edu]

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Checklist of New Zealand Ctenophora

Ctenophora in the following checklist pertain only to those in the Exclusive Economic Zone.

The following synopsis is based on the scheme proposed by Harbison (1996) for adult epipelagic forms from the North Atlantic, and that in Mills (2008). For diagnostic characters of the various taxa, see Mayer (1912), Liley (1958), Greve (1975), Harbison (1985, 1996), O'Sullivan (1986), and Harbison & Madin (1982). This classification is provisional and is very likely to change as more species and phylogenetic data are obtained.

E = endemic species; * = new record.

PHYLUM CTENOPHORA

Class TENTACULATA

Order CYDIPPIDA

EUPLOKAMIDAE

Euplokamis helicoides (Ralph & Kaberry, 1950) E

LAMPEIDAE

Lampea sp. Ralph 1950, as *Lampetia*

PLEUROBRACHIIDAE

Horniphora sp. Mills pers. obs. 1981

Pleurobrachia australis (Benham, 1907)

Pleurobrachia pileus (O.F. Müller, 1776)

Sabaudia liguriae Ghigi, 1909 E

INCERTAE SEDIS

Eschscholthia dimidiata (Eschscholtz, 1829) E

Order PLATYCTENIDA

COELOPLANIDAE

Coeloplana willeyi Abbott, 1902

Order LOBATA

BOLINOPSIDAE

Bolinopsis sp. Gordon & Ballantine 1977; Mills pers. obs. 1981

Lesueurina pinnata Ralph & Kaberry, 1950 E

EURHAMPHAEIDAE

Eurhamphaea sp.* [det. H. Mianzan from photo]

LEUCOTHEIDAE

Leucothea multicornis (Quoy & Gaimard, 1824)

BATHOCYROIDAE

Bathocyroe paragaster (Ralph & Kaberry, 1950) E

OCYROPSIDAE

Ocyropsis crystallina (Rang, 1828)

Order CESTIDA

CESTIDAE

Cestum veneris Lesueur, 1813

Velamen parallelum (Fol, 1869)*

Class NUDA

Order BEROIDA

BEROIDAE

Beroe cucumis Fabricius, 1780

Beroe forskalii Milne Edwards, 1841

Beroe ovata Bruguère, 1789