

REVIEW

Predation on pelagic coelenterates: a review

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Coelenterates (cnidaria and ctenophores) are well recognized as predators in food webs of marine ecosystems but are less often considered as prey. This is partly because they are digested very rapidly. In studies based on predator stomach contents the measured masses of different prey organisms are rarely scaled by their relative rates of digestion. Predators that are frozen and thawed, or for which whole stomachs are placed in preservatives, may have already lost much of their coelenterate content when they are examined. There is also a tendency to assume that gelatinous organisms, with their high water and salt content relative to organic content, are poor food. However, given the high rates of digestion (and presumably of assimilation) coelenterates may provide sources of energy comparable to better recognized prey such as arthropods. It is already becoming well documented that a number of cnidaria and ctenophores as well as fish utilize gelatinous organisms as prey. Data is accumulating more slowly on predation by a wide range of other carnivores such as molluscs, arthropods, reptiles and birds.

INTRODUCTION

The ecology of pelagic coelenterates (Cnidaria and Ctenophora) has been more extensively investigated in recent years. In spite of their fragility they are now well recognized by marine zoologists as including a significant biomass especially under bloom conditions. Abundant forms in the neuston of the tropics and temperate zones are the hydrozoan chondrophores such as *Veleva* and siphonophores. These may project partly into the air and form pleustonic rafts that are passively transported by winds. The oceanic water column includes holoplanktonic Hydrozoa (trachymedusae, narcomedusae, and siphonophores) as well as coronate Scyphozoa and Ctenophora. To these in neritic areas are added species with benthic stages in the life cycle such as anthomedusan and leptomedusan Hydrozoa and semaeostome and rhizostome Scyphozoa. The pelagic larvae of Anthozoa such as corals and Ceriantharia may contribute significant biomass locally. Most ctenophores are holoplanktonic and may be abundant both inshore and offshore. In spite of their abundance the recognized involvement of these coelenterates in pelagic food webs is not well balanced. Their role as important predators on marine animals such as other coelenterates, arthropods and larval fish has been extensively investigated and reviewed (Arai, 1988, 1997a,b; Purcell, 1991, 1997). Most are primarily documented as carnivores

feeding on macroscopic animals, although some utilize microzooplankton, near surface forms may possess symbionts, and a few have been shown to take up dissolved organic material (DOM) directly (Arai, 1997b). They are not, however, generally recognized as prey. A typical comment is that by Sommer et al. (2002); ‘Gelatinous zooplankton are usually considered a dead end in the pelagic food web because their low nutritional value makes them a minor food item for vertebrates, although there are some minor exceptions (e.g. the moon fish *Mola mola* and sea turtles).’ Coelenterates are indeed depicted incorrectly as dead ends in their paper on pelagic food web configurations. In fact there is already information in the literature showing that coelenterates are not dead ends and are preyed on by a number of types of animals as will be described below.

The most extensive data on predators to date are for other coelenterates and fish. The former was reviewed by Purcell (1991a) and the latter by Ates (1988) and Arai (1988) and by Purcell & Arai (2001). The present review updates the data on coelenterates and fish and also presents evidence for other groups such as molluscs, arthropods, reptiles and birds.

Although there may be visual observations such as those of *Mola mola* (Linnaeus, 1758) and turtles referred to by Sommer et al. (2002), most quantitative data comes from investigations of stomach contents of the

predator. These stomach contents are seldom scaled for comparative digestion rates as they logically should be. Even if stomachs are examined immediately the diet proportions of animals without resistant structures are underestimated. In addition predators are often stored by methods such as freezing or fixation of whole fish which allow loss of soft tissues before observations are made. In a few cases relatively resistant structures of coelenterates such as the ctenes of Ctenophora, the cnidae of Cnidaria or the sails of the Chondrophora may be examined.

Also, as in the quote, it is often considered that gelatinous animals can be ignored since they might constitute poor diets because of the low ratio of organic material to salt and water. The energy contents of coelenterates with large amounts of mesogloea have been difficult to measure accurately due to the high amount of salt and hence of bound water (Arai, 1997a). Typically they are reported with calorimetric values per unit of wet weight which are less than 20% of those of arthropods (Arai, 1988; Davis et al., 1998). On the other hand if two prey items of the same wet weight are compared this low energy content of the coelenterates may be compensated for by higher rates of digestion (and presumably assimilation) of gelatinous animals. This has been shown for chum salmon, *Oncorhynchus keta* (Walbaum, 1792), feeding on the ctenophore *Pleurobrachia* or on the same wet weight of shrimp, where rate of ctenophore digestion exceeded shrimp by over 20 times (Arai et al., 2003). Provided the fish has a good supply of prey to process at this high rate, the *Pleurobrachia* provide a good diet. Similar measurements need to be repeated on a number of predator–coelenterate prey combinations.

PREDATORS OF PELAGIC COELENTERATES

Cnidaria and Ctenophora

One important group of predators on pelagic coelenterates which has been reviewed by other authors is that of other coelenterates (Purcell, 1991a, 1997). Included among the hydromedusan predators are such pandeids anthomedusae as *Stomotoca*, leptomedusae such as *Aequorea*, and narcomedusae such as *Solmissus* (Arai & Jacobs, 1980; Larson et al., 1989; Purcell, 1991b; Raskoff, 2002). *Apolemia uvaria* (Leseuer, 1815) is an unusual siphonophore in that it consumes a significant amount of gelatinous prey including hydromedusae and ctenophores (Purcell, 1981). As discussed below many Scyphozoa prey on other scyphomedusae and on hydromedusae as well as on ctenophores. Benthic Anthozoa such as sea anemones may prey on pelagic

coelenterates at the bottom of the water column (Fautin & Fitt, 1991). Larvae of sea anemones such as *Edwardsia lineata* (Verrill, 1874) and *Peachia quinquecapitata* McMurrich, 1913 which infest ctenophores and medusae may feed only on the ingested food of the host or directly on the host tissue (Mills, 1993; Bumann & Puls, 1996). Finally the beroid ctenophores prey primarily on other ctenophores and the cydippid ctenophore *Haekelia* feeds on narcomedusae (Purcell, 1997).

Semaeostome scyphomedusae eat a broad range of plankton including fish and arthropods but also gelatinous prey such as other scyphomedusae, hydromedusae and ctenophores (Purcell, 1997). They may have major effects on the populations of some common coelenterate prey even when the prey has responses that allow a portion of them to escape. *Chrysaora quinquecirrha* (Desor, 1848) can eliminate the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 from tributaries of Chesapeake Bay even though adult *M. leidyi* can often increase swimming speed and escape with some loss of tissue (Purcell & Cowan, 1995; Kreps et al., 1997). Some semaeostomes are able to prey on other semaeostomes even though they may have developed escape responses. *Cyanea capillata* (Linnaeus, 1758) can capture *Aurelia aurita* (Linnaeus, 1758) of the same or smaller size even when the prey changes direction and swims faster (Bamstedt et al., 1994; Hansson, 1997). Similarly *Phacellophora camtschatica* Brandt, 1835 can only catch *Aurelia* of smaller size than the predator (Strand & Hamner, 1988).

Some coelenterates are dependent on other coelenterate prey for particular compounds or structures. *Aurelia aurita* ephyrae can be raised on diets of *Artemia* nauplii or mixed zooplankton. *Cyanea capillata* ephyrae, however, require gelatinous prey such as the ctenophore *Bolinopsis infundibulum* (O.F. Muller, 1776), *Aurelia*, or the hydromedusa *Phialella* even though the adults have a much broader diet (Bamstedt et al., 1997). *Aequorea victoria* (Murbach & Shearer, 1902) requires a diet including coelenterazine from other luminescent medusae or ctenophores in order to produce bioluminescence (Haddock et al., 2001). The ctenophore *Haekelia rubra* (Kolliker, 1853) incorporates cnidae from narcomedusan prey into their own tentacles (Carre et al., 1989).

There may be fairly complex food webs even within the coelenterate community of a single bay such as Departure Bay, British Columbia (Arai & Jacobs, 1980). Predation may be size dependent so that the roles of predator and prey may interchange and add to the complexity. For example, adults of the hydromedusa *Aequorea victoria* eat adult *Clytia gregaria* (L. Agassiz, 1862) but adult *C. gregaria* eat embryonic and larval *A. victoria* (see Pennington, 1990).

Many of the hydromedusae and scyphomedusae that eat coelenterates also eat other prey such as copepods. As pointed out by Purcell (1991a) this leads to a situation where medusae may exhibit intraguild predation, consuming species that potentially compete with them for food. Intraguild predation occurs in the scyphomedusa described above as preying on one another. It also occurs in predation by *Aequorea victoria* on other species of potentially competing hydromedusae, siphonophores and ctenophores (Purcell, 1991b).

Literature of digestion rates of the scyphozoan medusae *Aurelia aurita* and *Cyanea capillata* and the ctenophore *Bolinopsis infundibulum* feeding on various prey was summarized by Martinussen & Bamstedt (1999). They emphasized the increase in digestion times with increasing prey size. A subsequent paper considered the effects of temperature in their own data and the literature on other species. They found that increased temperatures clearly increased the rates of digestion by Ctenophora but that, with other sources of variation such as predator and prey type and size, no clear effect of temperature was shown for digestion by cnidarian predators (Martinussen & Bamstedt, 2001). Without standardization of experimental conditions and prey size, there was also no clear difference in digestion rates between gelatinous and non-gelatinous prey.

Helminths

Parasitic trematodes, cestodes and nematodes are widely distributed in hydromedusae, scyphomedusae and ctenophora (Lauchner 1980a,b; Purcell & Arai, 2001). Many of these are larvae of helminths which have complex life cycles in which the definitive host, where the parasite becomes sexually mature, are fish (Marcogliese, 1995). As more data is obtained on fish eating coelenterates it becomes better recognized that those coelenterates may be acting as intermediate hosts. Conversely parasites may help verify links in the marine food web (Marcogliese, 2002). The extent of predation on the coelenterates by the parasites has not yet been measured.

Molluscs

Among the Phylum Mollusca the best documented predators of pelagic coelenterates are the nudibranchs and snails of the Class Gastropoda. Most gastropods eat with the aid of a radula, a membranous belt bearing transverse rows of teeth which can be used in a scraping motion. The resulting stomach contents can be difficult to identify.

Nudibranchs most strongly influence the populations of pelagic coelenterates as predators on the benthic stages of scyphozoan and hydrozoan medusae. One example is that the predation of the nudibranch

Coryphella verrucosa (M. Sars, 1829) is the main factor regulating the populations of the polyps, and hence the release of ephyrae, of *Aurelia* in the fjords of western Sweden (Hernroth & Grondahl, 1985). There is an extensive literature on the specificity and dynamics of benthic predation and on the incorporation and utilization by the nudibranchs of the cnidae of the prey as protection (Todd, 1981; Harris, 1987; Frick, 2003). Both of those subjects and the production of benthic cysts as scyphozoan protection are outside the scope of the present review.

Observations of nudibranch and snail predation on pelagic coelenterates are largely concerned with predation on the neuston (Lalli & Gilmer, 1989). The glaucid nudibranchs, such as *Glaucus atlanticus* Forster, 1777 and *Glaucilla marginata* Bergh, 1868, are predators of the chondrophores *Veleva* and *Porpita* and the siphonophore *Physalia* (Thompson & Bennett, 1970). As with the benthic nudibranchs they are able to utilize the prey nematocysts, particularly from *Physalia*, and concentrate them in cnidosacs for defence (Thompson & Bennett, 1969; Bebbington, 1986). The nudibranch *Fiona pinnata* (Eschscholtz, 1831) also feeds on *Veleva* and concentrates its blue pigment (Kropp, 1931; Bayer, 1963). The shelled snails *Janthina* spp. construct rafts of bubbles which keep them at the surface and allow them to make floating contacts with prey such as *Veleva* and *Porpita* (Bieri, 1966; Pinn, 1980). In the water column the nudibranch *Cephalopyge trematoides* (Chun, 1889) feeds on the siphonophore *Nanomia*, and the heteropod *Carinaria cristata* forma *japonica* van der Spoel, 1972 also includes small siphonophores in its diet (Sentz-Braconnot & Carre, 1966; Seapy, 1980).

Predation by the squids and octopods of the Class Cephalopoda has also occasionally been observed. In addition to the radula these animals each possess a pair of powerful beak-like jaws in the buccal cavity and may secrete poison or proteolytic enzymes in the salivary glands. Although gelatinous tissue may be present in the stomach it is often difficult to identify its source. A *Veleva* was observed in the beak of a giant squid *Mortehuthis robusta* (Verrill, 1876) (see Smith, 1963). Twenty-two per cent of the prey weight in 17 stomachs of Market squid *Loligo opalescens* Berry, 1911 examined off Washington and Oregon in 1984 consisted of Cnidaria, primarily *Veleva* (Brodeur et al., 1987; Brodeur & Percy, 1992). Heeger et al. (1992) observed an octopod *Argonauta argo* Linnaeus, 1758 clasping and attacking a *Phyllorhiza* scyphomedusa.

Arthropods

The best recognized arthropod predators of pelagic coelenterates are the hyperiid amphipods of the Class

Malacostraca. Other predators in this class include gammaridean amphipods, euphausiids, mysids, and decapods such as crabs and shrimps. There is also predation by members of the Classes Copepoda, Ostracoda, Cirripedia (barnacles) and Pycnogonida.

Most hyperiid amphipods are known to be associated with gelatinous animals for some portion of their life cycle. New associations with medusae, ctenophores, siphonophores and salps continue to be discovered (e.g. Gasca & Haddock, 2004). They vary greatly in timing, degree of dependence of the hyperiids on their hosts for shelter or for food, and extent of maternal care. In many cases the post-embryonic development is completed in the host, and the juveniles are obligate parasites, dependent for food on their coelenterate hosts (Laval, 1980; Dittrich, 1987). Some adults, such as *Hyperia* spp., may remain facultative parasites eating some food of the medusae but with the gonads of the host scyphomedusae the preferred food (Dittrich, 1988, 1992; Buecher et al., 2001). *Parathemisto gaudichaudi* (Guerin) uses hydromedusae such as *Aglantha* as mating sites and as food, reaching a population peak a month after the hydromedusan population peaks (Scheader & Evans, 1975; Williams & Robins, 1981). *Themisto* spp. have wide ranging diets, and may be free-swimming or dependent on their hosts only for transportation (Condon & Norman, 1999). Population peaks are not correlated with those of *Aglantha* (Ikeda et al., 1992).

Gammaridean amphipods may also prey on coelenterates (Hopkins, 1985). The mesopelagic species *Parandania boeckii* (Stebbing, 1888) preys on *Atolla* spp. scyphomedusae (Moore & Rainbow, 1989). The species is morphologically specialized for feeding on coelenterates with broad shearing incisors, a narrow gate-like oesophagus and an extremely enlarged stomach (Coleman, 1990).

Decapods may both ride and prey on pelagic coelenterates. In the neuston the megalopae of the Dungeness crab *Cancer magister* Dana, 1852 may be free swimming but preferentially attach to *Velella* when it is present nearshore and feed on the hydroid (Wickham, 1979). In the water column shrimp such as *Bentheogennema* spp., *Gennadus* spp., *Notostomus* spp. and *Sergestes* spp. feed on siphonophores and coronate scyphomedusae (Hefferman & Hopkins, 1981; Roe, 1984; Nishida et al., 1988; Moore et al., 1993). On the other hand pandalid shrimp larvae may ride on hydromedusae without any predation (Marliave & Mills, 1993). Pelagic coelenterates may also sink towards the bottom allowing consumption by benthic predators. The common ctenophore *Pleurobrachia* drops near the sediment in winter and is captured by crabs and shrimps (Greve, 1972). The hermit crab *Pagurus bernhardos* (Linnaeus, 1758) modifies its feeding behaviour for this purpose,

searching and jumping. In the presence of these predators or of water inhabited by them the *Pleurobrachia* moves up away from the sediment (Esser et al., 2004). On the beach various crabs have been observed eating siphonophores *Physalia* and scyphomedusae *Stomolophus* and *Cyanea* which are in shallow water or stranded (Powell & Gunther, 1968; Farr, 1978).

Less data is available for other Malacostraca. Mysids such as *Eucopia unguiculata* (Willemoessuhm, 1875) may prey on coronate medusae as shown by nematocysts and pigmented epithelia observed in the foregut (Roe, 1984; Hopkins, 1985; Hopkins, 1987). There are also a few observations of coelenterate fragments in euphausiid stomachs (Hopkins, 1985, 1987; Hopkins & Torres, 1989). Beyer (1992) found *Meganyctiphanes norvegica* (M. Sars) eating the ctenophore *Pleurobrachia*.

Only scattered data is available for other classes of Arthropods. Coelenterate fragments have been found in copepods and ostracods (Hopkins, 1985, 1987; Hopkins & Torres, 1989). Greve (1972) showed that although adults of the ctenophore *Pleurobrachia* feed on copepods, there is also predation by *Calanus helgolandicus* Claus, 1863 on young stages of the *Pleurobrachia*.

In the Class Cirripedia the neustonic, pedunculate goose barnacles attach to floating debris or secrete a float (Cheng, 1975). *Lepas ansifera* Linnaeus, 1767 has independently movable cirri which allows it to manipulate a *Velella* or *Porpita* and strip the flesh from it (Bierri, 1966). Species of the genus *Alepas* are able to attach to the umbrellas of scyphozoan medusae using a specialized peduncle without cement (Pages, 2000). At least *Alepas pacifica* Pilsbury, 1907 feeds on the host medusa, especially on the gonads (Tabachnik, 1986; Pages, 2000).

Pycnogonid 'sea spiders' *Pallenopsis* (*Bathypallenopsis*) *scoparia* Fage, 1956 have been collected on the mesopelagic scyphomedusa *Periphylla* with nematocysts in their stomach contents (Child & Harbison, 1986). They have also been observed on hydromedusae but without data on stomach contents (Larson et al., 1991).

Chaetognaths

Early workers on the feeding of chaetognaths included medusae and siphonophores among the prey (see for example Alvarino (1985) and references therein). On the other hand Feigenbaum (1991) in his reviews of food and feeding behaviour considered that these reports were due to artefacts of the collection and fixation processes (Feigenbaum & Maris, 1984; Feigenbaum, 1991).

Fish

Fish are the group for which predation on coelenterate food is best documented (Arai, 1988; Ates, 1988;

Purcell & Arai, 2001). Table 1 of my previous review (Arai, 1988) included species of fish for which quantitative stomach content data indicated coelenterates in their diet at least for a particular time and place. The criteria for inclusion in the table was that coelenterates were present in at least 10% of the stomachs examined, or that coelenterates represented at least 5% of the volume, weight, or number of prey found in the stomachs. Only collections of 11 or more fish were included. Table 1 of the present review includes more recent different but similar data using the same criteria. The two tables include quantitative data from 69 species of fish in 34 families. This is only a small proportion of the fish actually utilizing coelenterates. There are probably species with eligible data that I missed from the scattered literature, and I found many more species that have been described without quantitative data. As more workers become aware of the necessity of speed in fixation of coelenterates the amount of data is rising quickly.

There are so far only a few fish for which coelenterates are the only known prey; even those with specialist diets may also eat hyperiid arthropods present on the prey or other gelatinous animals such as salps. There is therefore no sharp division between the specialists and the generalists. As noted by Ates (1988) and Harbison (1993) specialists include several species in the suborder Stromateoidei, especially from the families Centrolophoidae and Stromatidae, such as the commercially prized species of butterfly *Peprilus triacanthus* (Peck, 1804). The large number of generalists with broader diets include such commercial species as spiny dogfish *Squalus acanthias* Linnaeus, 1758, chum salmon *Oncorhynchus keta* (Walbaum, 1792), Atlantic mackerel *Scomber scombrus* Linnaeus, 1758 and various gadoids, scorpaenids and scombrids (Arai, 1988 and Table 1).

For deeper water Gartner et al. (1997) described trophic guilds of fish characterized by similar feeding habits. Among those four guilds containing species feeding on pelagic coelenterates, one guild of benthopelagic macronekton foragers with mixed diets includes a number of numerically dominant species such as grenadiers (Family Macrouridae), for example *Coryphaenoides*, some cod (Family Gadidae) and some slickheads (Family Alepocephalidae). Another guild of benthopelagic macroplanktonivores with specialized diets of gelatinous prey includes slickhead genera such as *Alepocephalus*. The gelatinous predator subguild of the pelagic zooplanktivores includes deep-sea smelts (Family Bathylagidae) whereas the guild of pelagic generalists includes some lantern fish (Family Myctophidae). These species may migrate into the upper levels at night. The dominant fish species in the midwater community of the subarctic Pacific is the myctophid

Stenobrachius leucopsarus (Eigermann & Eigermann, 1890) which often includes medusae, siphonophores or ctenophores in its generalist diet (Beamish et al., 1999). It migrates by night into the epipelagic waters and feeds on coelenterates in the epipelagic (0–200 m) and upper mesopelagic (200–500 m) zones but not in the lower mesopelagic zone (500–1000 m) of the Bering Sea (Gorbatenko & Il'inskii, 1992; Balanov et al., 1994).

The populations of pelagic coelenterates are often seasonal and the diets of the generalist predators usually reflect that. As an example Mianzan et al. (1996) examined 69 species from the Argentine continental shelf. They found that during the spring bloom of coelenterates 35% of the fish species included some ctenophores in their diet whereas during the other three seasons that figure fell to 15 to 23% of the fish species and the percentage frequency of gut contents also fell.

In other cases seasonal changes may reflect changes in currents. The seasonal food available to *Sebastes mystinus* (Jordan & Gilbert, 1881) off northern California depends on the pattern of upwelling and downwelling (Hobson & Chess, 1988). However, fish stomach contents do not always reflect seasonal prey abundance. Off Oregon, Brodeur et al. (1987) found that cnidaria were most common in *Squalus acanthias* stomachs in May but were most common in *Anoplopoma fimbria* (Pallas, 1814) stomachs in September although both fish species were primarily utilizing *Velella*. Anomalous seasonal differences in feeding may reflect changes in diet as fish grow; for example, chum salmon *Oncorhynchus keta* rarely eat gelatinous material in the first few weeks of life in salt water but begin to utilize coelenterates in later summer (King & Beamish, 2000).

The only paper on digestion rates of fish eating coelenterates is the study by Arai et al. (2003) of chum salmon *Oncorhynchus keta* eating the ctenophore *Pleurobrachia bachei* described in the Introduction. Further examination of digestion rates is needed so that stomach contents can be scaled by their relative rates of digestion. At present it is not possible to convert the data on stomach contents such as is given in Table 1 to feeding rates. Given the high digestion rates of gelatinous animals such feeding rates would be expected to demonstrate, better than the unscaled stomach content data discussed above, the relative value of coelenterate prey to the diets. It is also probable it will become more apparent that predation by the large number of fish with generalized diets including coelenterates is more ecologically important than the predation by the relatively small numbers of specialized fish with primarily gelatinous diets.

Various physical adaptations of fish predators to a jellyfish diet have been described. Some specialized

Table 1. Examples of fish predation on pelagic coelenterates based on stomach contents data (see also table 1, Arai, 1988).

Predator	Prey	Consumption rate*	Reference
Class CHONDRICHTHYES			
Family CARCHARINIDAE			
<i>Galeorhinus galeus</i> Jordan & Gilbert, 1883	<i>Verella</i>	24.8% p. no./ 14 st.	Brodeur et al., 1987
Family SQUALIDAE			
<i>Squalus acanthias</i> Linnaeus, 1758	<i>Verella</i>	94.2% p. no./ 23 st.	Brodeur et al., 1987
	Siphonophore	41.8% p. no./ 81 st.	Brodeur et al., 1987
	Cnidaria	50.2% p. wt./ 23 st.	Brodeur & Pearcy, 1992
	Ctenophora	44 obs./221 st. winter	Mianzan et al., 1996
	Ctenophora	23% p. no./ 262 st	Laptikhovsky et al., 2001
Family RAJIDAE			
<i>Bathyrhaja macloviana</i> (Norman, 1937)	Ctenophora	11 obs./64 st. spring	Mianzan et al., 1996
Class OSTEICHTHYES			
Family CLUPEIDAE			
<i>Alosa aestivalis</i> (Mitchell, 1814)	Ctenophora	43% p. wt./11 st.	Bowman et al., 2000
Family ARGENTINIDAE			
<i>Argentina silus</i> (Ascanius, 1775) 21–25 cm	Ctenophora	9.2% p. wt./24 st.	Bowman et al., 2000
Family BATHYLAGIDAE			
<i>Bathylagus antarcticus</i> Gunther, 1878	Siphonophores	14 obs./ 28 st.	Lancraft et al., 1991
<i>Bathylagus pacificus</i> Gilbert, 1890	Medusae	32.7% p. wt./50 st.	Balanov et al., 1995
	Medusae	13.0% p. wt./ 316 st.	Sobolevskii & Senchenko, 1996
	Ctenophore	48.7% p. wt./ 316 st.	Sobolevskii & Senchenko, 1996
<i>Leuroglossus schmidtii</i> Rass, 1955	Medusae	9.3% p. wt./210 st.	Gorbatenko & Il'inskii, 1992
	Medusae	8.95% p. wt./1291 st.	Il'inskii & Gorbatenko, 1994
	Ctenophore	8.3% p.wt./1291 st.	Il'inskii & Gorbatenko, 1994
	Cnidaria	9.2% p. wt./ 30 st. 0–200 m; 9.4% p. wt./180 st.	Balanov et al., 1994
	Medusae	24.5% p. wt./485 st. 200–500 m; 30% p. wt./ 49 st. 500–100 m	Balanov et al., 1995
	<i>Beroe</i>	5.3% p. wt./485 st. 200–500 m	Balanov et al., 1995
	Medusae	56.3% p. wt/ 510 st.	Sobolevskii & Senchenko, 1996
	Ctenophore	9.2% p. wt./ 510 st.	Sobolevskii & Senchenko, 1996
<i>Lipolagus ochotensis</i> (Schmidt, 1938)	Medusae	26.1% p. wt./985 st.	Il'inskii & Gorbatenko, 1994
	Ctenophore	36.15% p. wt./985 st.	Il'inskii & Gorbatenko, 1994
	Medusae	12% p. wt./283 st. 200–500 m; 30.8% p. wt/100 st. 500–1000 m	Balanov et al., 1995
	<i>Beroe</i>	9.5% p. wt./ 283 st. 200–500 m	Balanov et al., 1995
	Medusae	60% p. wt./ 179 st.	Sobolevskii & Senchenko, 1996
	Ctenophore	26.9% p. wt./ 179 st.	Sobolevskii & Senchenko, 1996
<i>Pseudobathylagus milleri</i> (Jordan & Gilbert, 1898)	Medusae	100% p. wt./40 st.	Balanov et al., 1995
	Medusae	85.7% p. wt./ 285 st.	Sobolevskii & Senchenko, 1996
	Ctenophore	8.7% p. wt./ 285 st.	Sobolevskii & Senchenko, 1996
Family ALEPOCEPHALIDAE			
<i>Alepocephalus rostratus</i> Risso, 1820	Pelagic coelenterates	37% p. no./128 st.	Carrasson & Matallanas, 1990
	Siphonophores	26.8% p. no/118 st. summer	Carrasson & Matallanas, 1998
Family SALMONIDAE			
<i>Oncorhynchus keta</i> (Walbaum, 1792) juvenile	Ctenophore	74 obs./ 580 st.	Healey, 1991
	<i>Beroe</i>	38.6% p. wt./ 47 st.	Sobolevskii & Senchenko, 1996
	Jellyfish	6% p. wt./267 st. 1991; 10% p. wt./168 st. 1992	Tadokoro et al., 1996
juvenile	Ctenophora	94 obs./ 260 st. 1997; 334 obs./ 699 st. 1998	King & Beamish, 2000
<i>Oncorhynchus kisutch</i> (Walbaum, 1792)	<i>Verella</i>	14 obs/ 87 st.	Brodeur et al., 1987
<i>Oncorhynchus nerka</i> (Walbaum, 1792)	Jellyfish	11% p. wt./42 st. 1991	Tadokoro et al., 1996
<i>Oncorhynchus clarki clarki</i> (Richardson, 1836)	Hydromedusae	2 obs. /16 st.	Brodeur et al., 1987
Family MYCTOPHIDAE			
<i>Ceratoscopelus warmingii</i> (Lutken, 1892)	Siphonophores	6–29% dry wt./ 114 st.	Hopkins & Gartner, 1992
<i>Diaphus mollis</i> Taning, 1928	Siphonophores	10–12 % dry wt./ 41 st.	Hopkins & Gartner, 1992

Table 1. (*continued.*)

<i>Stenobrachius leucopsarus</i> (Eigermann & Eigermann, 1890)	Medusae	8.1% p. wt./ 90 st. 0–200 m; 8.8% p. wt./ 180 st. 200–500 m; 0 p. wt./ 100 st. 500–1000 m	Gorbatenko & Il'inskii, 1992; Balanov et al., 1994
<i>Stenobrachius nannochir</i> (Gilbert, 1890)	Medusae	6.6% p. wt./ 385 st.	Il'inskii & Gorbatenko, 1994
	Medusae	8.9% p. wt./ 343 st.	Balanov et al., 1995
	Medusae	14.2% p. wt./ 396 st.	Sobolevskii & Senchenko, 1996
Family GADIDAE			
<i>Pollachius virens</i> (Linnaeus, 1758)	Medusae	23 obs./133 st.	Hall et al., 1990
Family SCOMBERESOCIDAE			
<i>Scomberesox saurus</i> (Walbaum, 1792)	Siphonophora	54.4% p. wt./30 st.	Bowman et al., 2000
Family SCORPAENIDAE			
<i>Helicolenus dactylopterus</i> (Delaroche, 1809)	Ctenophora	130 obs./273 st. spring/summer	Mianzan et al., 1996
<i>Sebastes flavidus</i> (Ayres, 1862)	Cnidaria	2 obs./ 14 st.	Brodeur et al., 1987
<i>Sebastes melanops</i> Girard, 1856	Pleurobrachia	13.3% p. wt./ 30 st.	Brodeur et al., 1987
	<i>Beroe</i>	13.3% p. wt./ 20 st.	Brodeur & Pearcy, 1992
<i>Sebastes mystinus</i> (Jordan & Gilbert, 1881)	<i>Velella</i>	8 obs./ 51 st.	Hobson & Chess, 1988
	<i>Stephanomia</i>	11 obs./ 73 st.	Hobson & Chess, 1988
	<i>Pleurobrachia</i>	20 obs./ 73 st.	Hobson & Chess, 1988
	Scyphozoa	12 obs./ 73 st.	Hobson & Chess, 1988
	<i>Muggiaea</i>	4 obs./ 12 st.	Hobson et al., 1996
	<i>Stephanomia</i>	6 obs./ 12 st.	Hobson et al., 1996
	<i>Beroe</i>	4 obs./ 12 st.	Hobson et al., 1996
Family ANOPILOMATIDAE			
<i>Anoplopoma fimbria</i> (Pallas, 1814)	<i>Velella</i>	12.4% p. wt./ 98 st.	Brodeur et al., 1987
	Cnidaria	14.4% p. wt./ 35 st.; 19.3% p. wt./ 16 st.	Brodeur & Pearcy, 1992
	Scyphomedusae	9.54% p. wt./ 331 st. 1990; 8.89% p. wt./ 355 st. 1993; 13.5% p. wt./ 72 st. 1996	Yang & Nelson, 2000
Family HEXAGRAMMIDAE			
<i>Pleurogrammus monopterygius</i> (Pallas, 1810)	Scyphomedusae	19% p. wt./ 42 st.	Yang & Nelson, 2000
Family TERAPONIDAE			
<i>Terapon theraps</i> (Cuvier, 1829)	Siphonophora	22 obs./57 st.	Senta et al., 1993
Family CARANGIDAE			
<i>Trachurus murphyi</i> Nichols, 1920	Siphonophora	27.7% p. wt./ 57 st.	Nevin, 2004
Family SCIAENIDAE			
<i>Microgogonias furnieri</i> (Desmarest, 1823)	Ctenophora	37 obs./350 spring	Mianzan et al., 1996
Family KYPHOSIDAE			
<i>Kyphosus cinerascens</i> (Forsskal, 1775)	Siphonophora	20 obs./54 st.	Senta et al., 1993
<i>Kyphosus vaigiensis</i> (Quoy & Gaimard, 1825)	Siphonophora	40 obs./47 st.	Senta et al., 1993
Family EPHIPPIDIDAE			
<i>Chaetodipterus faber</i> (Broussonet, 1782)	<i>Chiropsalmus</i>	9.4% vol./ 177 st.	Hayse, 1990
Family POMACENTRIDAE			
<i>Abudefduf vaigiensis</i> (Quoy & Gaimard, 1825)	Siphonophora		Senta et al., 1993
Family ZOARCIDAE			
<i>Bothrocara microcephala</i> (Schmidt, 1938)	Medusae	7.9% p. wt./190 st.	Il'inskii & Gorbatenko, 1994
<i>Lycogrammoides schmidtii</i> Soldatov & Lindberg, 1929	Medusae	9.45% p. wt./162 st.	Il'inskii & Gorbatenko, 1994
Family NOTOTHEIIDAE			
<i>Lepidonotothen squamifrons</i> (Gunther, 1880)	Ctenophora	0–48.8% p. wt./ 50–2231 st. depending month	Pakhomov, 1993
	Medusae	0.91–9.2% p. wt./ 14,319 st. depending season	Pakhomov, 1993
<i>Patagonotothen ramsayi</i> (Regan, 1913)	Ctenophora	15 obs./81 st. spring	Mianzan et al., 1996
	<i>Mnemiopsis</i>	52.9% p. no./ 81 st. summer	Laptikhovskiy & Arkhipkin, 2003
Family CENTROLOPHIDAE			
<i>Seriotelella porosa</i> Guichenet, 1848	Ctenophora	62 obs./133 st. spring/summer	Mianzan et al., 1996
Family STROMATEIDAE			
<i>Peprius triacanthus</i> (Peck, 1804) 6–10 cm	Cnidaria	8.7% p. wt./327 st.	Bowman et al., 2000
<i>Stromateus brasiliensis</i> Fowler, 1906	Ctenophora	216 obs./285 st. spring/summer	Mianzan et al., 1996
Family BALISTIDAE			
<i>Canthidermis maculata</i> (Block, 1786)	Siphonophora	18 obs./66 st.	Senta et al., 1993

*, st. stomachs examined; obs., stomachs in which coelenterate prey was observed; p. prey; no., number; vol., volume; wt., weight.

fish such as the stromateoid species may have deep bodies and underslung jaws (Harbison, 1993) but those with generalized diets such as mackerel may be much more streamlined. More widely correlated with a gelatinous diet is enlargement of the digestive tract, either stomach or intestine; for example chum salmon utilize more gelatinous prey than other *Oncorhynchus* species and the stomach is larger than other species of the genus (Welch, 1997). There are often also oesophageal or pharyngeal modifications to prevent regurgitation, to carry out trituration or to protect against nematocysts (Purcell & Arai, 2001).

Reptiles

Stomach contents of small numbers of specimens show that several species of marine turtles eat diets including jellyfish and their commensals and prey (Bjorndahl, 1997). Green turtles *Chelonia mydas* (Linnaeus, 1758) feed primarily on sea grasses and algae although they may also eat chondrophores, jellyfish, salps and sponges. Loggerhead turtles *Caretta caretta* (Linnaeus, 1758) eat the coelenterates *Velella*, siphonophores such as *Physalia*, scyphomedusae, and ctenophores but also a broad range of other prey including salps, molluscs, barnacles, crustacea, benthic crabs and fish. The leatherback turtle *Dermochelys coriacea* (Vandelli, 1761), has been shown to eat a more exclusively gelatinous diet including salps and pyrosomes, large siphonophores such as *Apolemia*, and medusae. Scyphomedusae observed in stomach contents of leatherbacks from different areas include *Aurelia*, *Catostylus*, *Chrysaora*, *Cyanea*, *Pelagia*, *Rhizostoma*, and *Stomolophus*. Leatherback hatchlings have been reared for six months on the scyphomedusa *Cassiopea* (Witham & Futch, 1977). Posthatchlings have been observed eating ctenophores and *Aurelia* using visual and chemical cues (Constantino & Salmon, 2003; Salmon et al., 2004).

Physiologically leatherback turtles are very interesting because they can use a jelly diet not only to carry out metabolism and growth but also to maintain endothermy. They are able to sustain core temperatures of around 25°C in water temperatures down to 5°C (Davenport, 1998). This means that they must also expend energy raising the temperature of the food to core temperature. The large body size (and consequent low surface:volume ratio), thick layer of subcutaneous fat and countercurrent heat exchangers in the flippers conserve heat. The turtles must still eat a very high volume of gelatinous food to sustain the energy drains. Adaptations to handling large volumes of gelatinous food include a very large, looped oesophagus with cornified conical spines and a compartmentalized stomach (Den Hartog & Van Nierop, 1984).

In order to find their food marine turtles can migrate long distances following fronts and other areas where there are near surface concentrations of coelenterates. Leatherbacks can also dive to at least 500 m and spend much of their time submerged (Eckert et al., 1989; Southwood et al., 1999; Hays et al., 2004). Feeding on scyphozoa has been observed directly at the surface (Eisenberg & Frazier, 1983; Grant & Ferrel, 1993; James & Herman, 2001). Little is as yet known about the presumed deeper foraging.

Birds

Most studies of diets of marine birds have been conducted during the summer at breeding colonies when adults return to feed dependent offspring (Shealer, 2001). Birds may be killed to obtain stomach data or regurgitations may be observed. The regurgitations fed to the chicks may differ from the diet of the adults. Due to the rapid breakdown of gelatinous tissue, predation on jellyfish was not recognized as significant until Harrison (1984) found scyphozoan tissue in stomachs of 11 out of 17 species of marine birds shot in the Bering Sea. Subsequent work has shown that many sea birds particularly of the order Procellariiformis and the Families Alcidae and Laridae of the Order Charadriiformes in the Bering Sea and northern Atlantic Ocean feed substantially on nearsurface gelatinous plankton including scyphomedusae and the ctenophore *Beroë*. In warmer waters chondrophores such as *Velella* are utilized as well.

The diet and feeding ecology of marine birds in the Order Procellariiformis were reviewed by Prince & Morgan (1987). The order includes the fulmars, diving petrels, albatrosses, shearwaters, petrels and storm-petrels. Many of these species are adapted for long-distance flight although the diving petrels have stocky bodies with a 'whirring' flight which can be continued underwater.

The northern fulmar *Fulmaris glacialis* (Linnaeus, 1761) has a catholic diet which includes zooplankton, squid, fish and fishery waste. Over 42% of the 136 stomachs examined by Harrison (1984) in the Bering Sea contained scyphozoan tissue; see also similar data in Schneider et al. (1986). Some meals delivered to chicks consist entirely of jellyfish (Hatch, 1993). Off the Isle of Man fulmars were watched feeding at the surface on the scyphozoa *Aurelia*, *Cyanea*, and *Rhizostoma*, together with the ctenophores *Beroë* and *Pleurobrachia* (McCanch & McCanch, 1996). Regurgitated material from the proventriculus (fore-stomach) of live specimens at the breeding colony on St Kilda, north-west of the United Kingdom, included whole skeletons of *Velella* (Ates, 1991; Camphuysen & van Franeker, 1996).

Storm-petrels 'patter' along the surface when feeding or make shallow plunges rather than sitting on the water as the other members of the order do. Harrison (1984) found scyphozoan tissue in 15 of 55 stomachs of the fork-tailed storm-petrel *Oceanodroma furcata* (Gmelin, 1789). *Verella* has been found in regurgitates of other storm-petrels (Vermeer & Devito, 1988; D'Elbee & Hemery, 1998). Shearwaters may sit on the surface but may also dive for some meters underwater. Harrison (1984) found scyphozoan tissue in six of 26 stomachs of the short-tailed shearwater *Puffinus tenuirostris* (Temminck, 1835); see also similar data in Schneider et al. (1986). *Verella* is included in the diet of the sooty shearwater *Puffinus griseus* (Gmelin, 1789) as noted by Ogi (1984) and Shiomi & Ogi (1992). Albatross feed by seizing objects at the water surface. Off Hawaii *Verella* were present in 9.8% of stomachs of 183 Laysan albatross *Phoebastria immutabilis* (Rothschild, 1893) (see Harrison et al., 1983).

The feeding of the Family Alcidae (auks, murre, puffins, guillemots, murrelets, and auklets) was reviewed by Vermeer et al. (1987). Alcids use pursuit diving to forage mostly for fish and/or zooplankton. Harrison (1984) noted that of 21 stomachs of the common murre *Uria aalge* (Pontoppidan, 1763) four contained scyphozoan tissue. In the Bering Sea parakeet auklets *Aethia psittacula* (Pallas 1769) differ from two other species in more extensive utilization of scyphomedusae and ctenophores, beyond that expected from predation on accompanying hyperiid amphipods (Harrison, 1990; Hunt et al., 1993, 1998). Harrison speculated that the unusual narrow hooked lower mandible of the bill and dispersed feeding pattern of this species may be associated with this diet.

Members of the Family Laridae (jaegers, skuas, gulls, kittiwakes and terns) may be scavengers at sea or on the beach, or may prey on live near-surface organisms. Harrison (1984) examined 32 stomachs of the black-legged kittiwake *Rissa tridactyla* (Linnaeus, 1758) and found scyphozoan tissue in 12 of them. Gulls and other shore birds have been observed pecking at the gonads of stranded *Aurelia* (Ates, 1991).

Mammals

The only mammals known to eat jellyfish are humans. Rhizostome scyphozoa are eaten by the cultures of the west Pacific Ocean rim from Korea to Thailand but especially in China and Japan. The traditional Chinese fishery in Hangzhou Bay reached a peak in 1966 and then declined precipitously due to pollution and overfishing (Liu et al., 1991). The Chinese are now raising scyphozoa by aquaculture at

other locations (Wang et al., 1991). Meanwhile the scyphozoa are being fished in south-east Asia (Omori & Nakano, 2001) and as far afield as Australia and the southern United States (Kingsford et al., 2000; Hsieh et al., 2001) to supply the Asian markets.

TROPHIC IMPLICATIONS

Having shown that predation on coelenterates is widespread, the next question is whether it is quantitatively important in the general pelagic food webs, outside of the interactions between various coelenterates. The most striking demonstration that it can be was the recent introduction of *Beroe ovata* into the Black Sea. Together with eutrophication and overfishing, introduction of the ctenophore *Mnemiopsis leidyi* in the early 1980s had been a major factor in the decrease of plankton previously used by fish and also in direct predation on fish eggs and larvae (Kideys, 2002). Since 1997 there has been a further introduction of *Beroe* which by the summer of 1999 was removing up to 10% of the *M. leidyi* population daily (Shiganova et al., 2001). The reduction in the population of *M. leidyi* in turn allowed a dramatic increase of 5-fold in the mesozooplankton and 20-fold in the ichthyoplankton. These remained at their higher levels to at least 2001 (Finenko et al., 2003). Less dramatically, predation of *M. leidyi* by the scyphozoan medusa *Chrysaora quinquecirrha* in Chesapeake Bay may also be followed by an increase in copepod abundance (Feigenbaum & Kelly, 1984; Purcell & Cowan, 1995).

In recent years there has been speculation on the possible causes of jellyfish population explosions or 'blooms' (Parsons & Lalli, 2002; Sommer et al., 2002; and papers cited therein). These authors generally discount the idea of top-down control of jellyfish populations, other than by other coelenterates, as being of importance. It is unlikely that reduction of predation by marine birds or turtles would have any significant effect on the populations of coelenterates on which they prey. However, as populations of fish are decreased by overfishing more instances are evident where increases in coelenterates may be due to release from predation. For instance long before the *Mnemiopsis* introduction *Aurelia aurita* was already increasing in the Black Sea in the 1970s. This may have been partly due to the removal of Atlantic mackerel *Scomber scombrus* by overfishing by the end of the 1960s as suggested by Zaitsev & Polischuk (1984).

Conversely increases of coelenterates may allow populations of fish preying on those coelenterates to increase. One example is the increase in abundance of *Aurelia* in the Inland Sea of Japan. In portions of the sea where *Aurelia* increase is high, catch of the butterfish *Psenopsis anomala* is also increasing (Uye & Ueta, 2004).

I hope that if the awareness of predation on coelenterates rises it will be further investigated and the results incorporated into models of pelagic food webs. To do that there needs to be routinely faster fixation (not freezing) of stomach contents of predators, and examination of the contents for nematocysts and ctenes as well as whole prey. There also needs to be much further examination of digestion rates and their implications for the comparative importance of prey found in the stomachs.

One fruitful area might be to trace the organic compounds released when blooms of jellyfish die. When medusae have spawned they may lose the ability to feed, and hence regenerate, and die. In small coastal water bodies there may be a large benthic deposit of organic material. Hyperiid amphipods are associated with mortality of inshore hydrozoa and scyphozoa (Dittrich, 1988; Mills, 1993). There has as yet been no study documenting what proportion of the organic compounds released are utilized by the amphipods or other predators which multiply at this time.

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