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Note

Benthic scavengers and predators of jellyfish, material for a review

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Abstract: Instances of predation and scavenging of jellyfish (pelagic Scyphozoa, Hydrozoa and Ctenophora) by benthic invertebrates are reviewed and presented. Sea anemones and decapod crabs are widespread as well as common predators or scavengers of jellyfish. Dead or dying jellyfish are also preyed upon by species of Echinodermata.

Key words: Actiniaria, Decapoda, Echinodermata, predation, scavenging, Scyphozoa, Hydrozoa, Ctenophora

Over the past decades the interaction between jellyfish and other animals received some attention (e.g. Arai 2005). Evidence had become available countering the previous prejudiced ideas about the negligible number of animal species preying on jellyfish. Nevertheless, jellyfish continue to be depicted occasionally (see Arai 2005 for examples) as dead ends in the food chains of the sea and/or as a rare source of food for predators (e.g. Condon et al. 2011), despite an increasing number of species of fishes (Redeke 1911, Luttenberger 1981, Gorelova & Grudtsev 1986, Kelley 1987, Ates 1988, Arai 1988, Zann 1988: 208, Cerqueira & Haimovici 1990, Hall 1992, Harbison 1993, Massuti et al. 1998, Purcell & Arai 2001, Bonaldo et al. 2004, Arai 2005, Orsi Relini et al. 2010a, Orsi Relini et al. 2010b, Chaves et al. 2010, Thaler 2012, Cardona et al. 2012, Milisenda et al. 2014, Battaglia et al. 2014, Sweetman et al. 2014, Dias & Almeida 2015), birds, reptiles and mammals (Dathe 1989, Ates 1991, Gronert 1992, Shiomi & Ogi 1992, Bell 1996, Zonfrillo 1997, Peglow 1998, Corsi 2000, Arai 2005, Suazo 2008, Cardona et al. 2012, Jarman et al. 2013, Melville 2013, Jones & Seminoff 2013), other cnidarians and ctenophores (Purcell 1991, Bamstedt et al. 1997, Bayha et al. 2012), polychaetes, helminths, molluscs and arthropods (Arai 2005, Stoner & Layman 2015) known to take them as prey.

Invertebrate species belonging to other groups have infrequently been mentioned as predators or scavengers of jellyfish. However, scuba-divers may encounter benthic animals consuming live or dead jellyfish on a regular basis. In Table 1 all records of sea anemones, corals, decapod crabs and echinoderms consuming live or dead jellyfish, known to me from the literature or otherwise, are listed.

Jellyfish (pelagic Scyphozoa, Hydrozoa and Ctenophora) easily fall victim to benthic invertebrate predators such as sea anemones. For about thirty years I have been able to observe for example *Metridium senile* taking jellyfish, mainly *Aurelia aurita, Cyanea lamarckii* and *Pleurobrachia pileus*, in considerable numbers in the Oosterschelde estuary, southwestern Netherlands (unpublished observations). Although the predation and the scavenging of jellyfish appears not to be limited geographically, most records in Table 1 are from eastern Atlantic waters, doubtlessly because I am more familiar with the grey literature in Europe.

The predominant prey mentioned in Table 1 taken by sea anemones, decapod crabs and echinoderms alike appear to be species of Scyphozoa. Observations of *Pleurobrachia, Neoturris, Eutonina, Eucheilota* and even scyphozoan ephyrae (see Table 1) make clear that this predation is however not size-limited. As the consumption time of the larger jellyfish exceeds several times that of the mostly much smaller hydrozoans and ctenophores, the likelihood of encountering Scyphozoa being consumed is much higher.

Few records in Table 1 go beyond the mere noting of the actual consumption of the jellyfish. In fact many of them have a casual or even tentative character. For patterns to be recognized more detailed observations need to be published. Hopefully future observers will publish more data pertaining to their observations of jellyfish being eaten. Berryman (1984) suggested that the predation by the sea anemone *Sagartiogeton laceratus* on *A. aurita* may become noteworthy when swarms of jellyfish are locally concentrated due to currents and topography. However, when scuba-diving, predation by sea anemones sensu latu upon jellyfish may be observed in each and every location where the two occur together. When

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Table 1. Benthic Cnidaria, decapod Crustacea and Echinodermata recorded to have consumed live or dead jellyfish.

PREDATOR OR SCAVENGER	PREY	LOCALITY	SOURCE
Cnidaria Actiniaria			
Actinia equina (Linnaeus, 1758)	*Pleurobrachia pileus* (Müller, 1776)	North Sea	Den Hartog 1963
A. equina	*Cyanea lamarckii* Péron & Lesueur, 1810	Channel Islands, England	S. Daly in: Wood 2013
Actinia tenebrosa Farquhar, 1898	Scyphozoa	Australian waters	Ayre 1984
Actinoporus elegans Duchassaing, 1850	*Aurelia ?*	Curaçao, Caribbean	Van der Vlugt 1981*
Actinostola callosa (Verrill, 1882)	*Periphylla periphylla* (Péron & Lesueur, 1810)	Norwegian waters	Jarms & Tiemann 2004
Anthopleura elegantissima (Brandt, 1835)	*Velella velella* (Linnaeus, 1758)	northeastern Pacific	Francis 1973; Wertheim 1984
Diadumene cincta Stephenson, 1925	*Eutonina indicans* (Romanes, 1876)	Oosterschelde, Netherlands	pers. comm. M. Vestjens 2002
Diadumene leucolena (Verrill, 1866)	*Chrysaora quinquecirrha* (DeSor, 1848)	western Atlantic	Cargo & Schultz 1967*; Cones & Haven 1969
Metridium farcimen (Brandt, 1835)	*Cyanea capillata* (Linnaeus, 1758)	northeastern Pacific	pers. comm. R. Harbo 2012
Metridium senile (Linnaeus, 1767)	*Aequorea victoria* (Murbach & Shearer, 1902)	northeastern Pacific	pers. comm. C.E. Mills 2000
M. senile	hydroid fragments	western Atlantic	Sebens & Koehl 1984
M. senile	*Aurelia aurita* (Linnaeus, 1758)	Grevelingen, Netherlands	this paper, see photo B
M. senile	*A. aurita, P. pileus, Chrysaora hysoscella* (Linnaeus, 1767)	Oosterschelde, Netherlands	Ates 2002
M. senile	*P. pileus*	North Sea	Greve 1972*
Paraphelliactis pabista Dunn, 1982	medusae?	northeastern Pacific	Fautin 1982
Sagartia sp.	*P. pileus*	North Sea	Greve 1972*
Sagartia elegans (Dalyell, 1848)	*C. hysoscella*	Oosterschelde, Netherlands	this paper, see photo C
Sagartia troglodytes (Price in Johnston, 1847)	*A. aurita, C. lamarckii, C. hysoscella*	Oosterschelde, Netherlands	Ates 2002
S. troglodytes	*E. indicans*	Oosterschelde, Netherlands	Ates 2014
Sagartiogeton laceratus (Dalyell, 1848)	*A. aurita*	North Sea	Berryman 1984
Sagartiogeton undatus (Müller, 1788)	*Aequorea vitrina* Gosse, 1853	Grevelingen, Netherlands	this paper, see photo D
S. undatus	cf. *Eucheilota*	Oosterschelde, Netherlands	pers. obs. July 2007
Urticina lofotensis (?)	*Aurelia labiata* Chamisso & Eysenhardt, 1821, *Phacellophora camtschatica* Brandt, 1835	?	pers. comm. P. Lovejoy Sept. 2000
Urticina felina (Linnaeus, 1761)	*Rhizostoma pulmo* (Macri, 1778), *P. pileus*	North Sea	Den Hartog 1963
U. felina	*P. pileus*	North Sea	Greve 1972*
U. felina	jellyfish (*Aurelia* ?)	Scottish waters	Wood 2005
U. felina	*A. aurita, C. lamarckii, C. hysoscella*	Oosterschelde, Netherlands	Ates 2002
U. felina	*C. hysoscella*	North Sea	Schwanitz, in Jarms & Tiemann 2004
U. felina	*A. aurita*	southwestern Ireland	pers. comm. W. Northway, May 2011
Urticinopsis antarcticus (Verrill, 1922)	jellyfish	Antarctic	Dayton et al. 1974
U. antarcticus	*Desmonema* sp.	Antarctic	Conniff 2000
sea anemone	*Mastigias ?*	Lake Kakaban, Indonesia	this paper, see photo E
Entacmaea(?) *medusivora* Fautin & Fitt, 1991	*Mastigias papua* (Lesson, 1830), *A. aurita, Cassiopea ornata* Haeckel, 1880	Lake Kakaban, Indonesia	Hoeksema et al. 2014
sea anemones	*M. papua*	Palau, western Pacific	Hamner 1982
Aiptasia pulchella(?) = *E.*(?) *medusivora*	*M. papua*	Palau, western Pacific	Hamner & Hauri 1981; Fautin & Fitt 1991
sea anemones	*A. aurita* ephyrae	Waddenzee, Netherlands	Swennen 1956*
sea anemone	*Nemopilema nomurai* Kishinouye, 1922	Sea of Japan	Yamamoto et al. 2008
Cnidaria other than Actiniaria			
Alcyonium digitatum Linnaeus, 1758	*P. pileus*	North Sea	Greve 1972*
Cerianthus lloydii Gosse, 1859	cf *Neoturris pileata*	Scottish waters	this paper, see photo A
Fungia scruposa Klunzinger, 1879	*A. aurita*	Red Sea	Alamaru et al. 2009
Tubularia sp.	*Lensia* sp.	?	Mackie 1966
Tubularia larynx Ellis & Solander, 1786	gelatinous plankton	Irish Sea	Gili et al. 1996

Table 1. Continued.

PREDATOR OR SCAVENGER	PREY	LOCALITY	SOURCE
Crustacea Decapoda			
Aristeomorpha foliacea (Risso, 1827)	Siphonophora	NW-Australia	Rainer 1992
Aristeus virilis (Bate, 1881)	Siphonophora	NW-Australia	Rainer 1992
Callinectes sapidus (Rathbun, 1896)	*C. capillata, Stomolophus meleagris* (Agassiz, 1862)	Gulf of Mexico	Farr 1978
Cancer pagurus Linnaeus, 1758	*A. aurita*	North Sea	Steinich 1973
Cancer sp.	*Linuche* sp.	Caribbean	Larson 1991
Carcinus maenas (Linnaeus, 1758)	*P. pileus*	North Sea	Greve 1972; Esser et al. 2004*
C. maenas	*A. aurita*	Kattegat	Rasmussen 1973
C. maenas	*A. aurita*	Baltic Sea	Lauckner 1980
Crangon crangon (Linnaeus, 1758)	*P. pileus*	North Sea	Greve 1972*; Esser et al. 2004*
Chorilia longipes Dana, 1852	*C. capillata*	northeastern Pacific	Harbo 2011
Galathea squamifera Leach, 1814	*P. pileus*	North Sea	Greve 1972*
Haliporoides sibogae (De Man, 1907)	Siphonophora	NW-Australia	Rainer 1992
Heterocarpus sibogae De Man, 1917	Siphonophora	NW-Australia	Rainer 1992
Heterocarpus woodmasoni Alcock, 1901	Siphonophora	NW-Australia	Rainer 1992
Homarus gammarus (Linnaeus, 1758)	*A. aurita*	Grevelingen, Netherlands	pers. comm. J. Bakker June 2013
Hyas araneus (Linnaeus, 1758)	*C. capillata*	Scottish waters	Ates & Hoyinck 2012
H. araneus	*A. aurita*	Scottish waters	pers. comm. W. Northway May 2011
Jasus lalandii (Milne-Edwards, 1837)	hydromedusae	?	Williamson, in Thomas 1963*
Liocarcinus depurator (Linnaeus, 1758)	*C. capillata*	Scottish waters	pers. comm. W. Northway Sept 2013
Menippe mercenaria (Say, 1818)	*Stomolophus*	Gulf of Mexico	Powell & Gunter 1968
Munida rugosa (Fabricius, 1775)	*A. aurita*	Scottish waters	Naylor 2011
Necora puber (Linnaeus, 1767)	*C. lamarckii*	Oosterschelde, Netherlands	this paper, see photo F
N. puber	*A. aurita*	Scottish waters	pers. comm. W. Northway Sept 2013
Ocypode quadrata (Fabricius, 1787)	*Physalia physalis* (Linnaeus, 1758)	Gulf of Mexico	Phillips et al. 1969
Pagurus anachoretus Risso, 1827	*Pelagia noctiluca* (Forskål, 1775)	Mgar-Ix-Ieni, Gozo, Malta	this paper, see photo G
Pagurus bernhardus (Linnaeus, 1758)	*P. pileus*	North Sea	Greve 1972*; Esser et al. 2004*
P. bernhardus	*A. aurita*	Scottish waters	Ates & Hoyinck 2012; this paper, see photo H
P. bernhardus	*C. capillata*	Scottish waters	pers. comm. W. Northway Sept 2013
Pagurus floridanus (Benedict, 1892), *Pagurus pollicaris* Say, 1817	*Cyanea, Stomolophus*	Gulf of Mexico	Phillips et al. 1969*
Portunus holsatus Fabricius, 1798	*P. pileus*	North Sea	Greve 1972*
Plesiopenaeus edwardsianus (Johnson, 1868)	Siphonophora	NW-Australia	Rainer 1992
Pugettia producta (Randall, 1840)	jellyfish	northeastern Pacific	pers. comm A. Lamb 2012
Scyphax ornatus Dana, 1853	*Physalia, A. aurita, Velella*	New Zealand intertidal	Quilter 1987
Crustacea other than Decapoda			
Balanus eburneus Gould, 1841	*C. quinquecirrha* ephyrae	western Atlantic	Cones & Haven 1969
Orchomenella obtusa (Sars, 1891), *Munida tenuimana* Sars, 1872, *decapod shrimps*	*P. periphylla, C. capillata*	Norwegian waters	Sweetman et al. 2014
Echinodermata			
Asterias rubens Linnaeus, 1758	*C. capillata*	Norwegian waters	Moen & Svensen 2000
A. rubens	*A. aurita*	Scottish waters	Ates & Hoyinck 2012
Ophiocomina nigra (Abildgaard, 1789)	*A. aurita*	Scottish waters	Ates & Hoyinck 2012
O*phiothrix fragilis* (Albildgaard, 1789)	*A. aurita*	Oosterschelde, Netherlands	Ates 2002
O. fragilis	*A. aurita*	Scottish waters	Ates & Hoyinck 2012
seastar (Anseropoda ?)	jellyfish	California	Wu 1998
Strongylocentrotus franciscanus (Agassiz, 1863)	jellyfish	northeastern Pacific	pers. comm. A. Lamb 2012
ophiurids	*Aurelia limbata* (Brandt, 1835)	Sea of Japan	Miyake et al. 2002

* aquarium observation

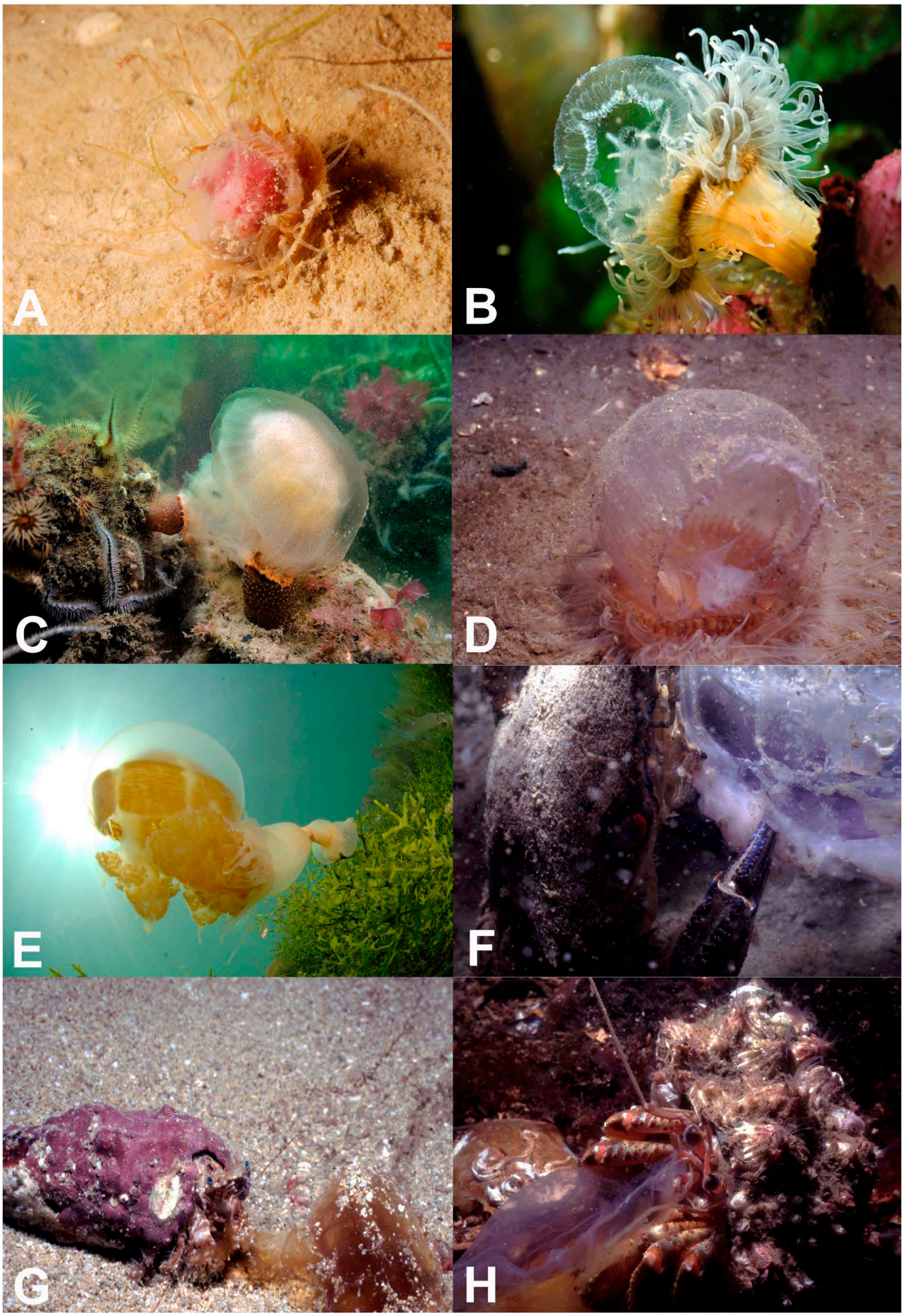

Plate 1.

offered a jellyfish, in an experimental context under water, a sea anemone will rarely fail to grab and devour it. In deeper water beyond the reach of scuba-divers, sea anemones are also known to prey heavily on jellyfish (Jarms & Tiemann 2004). As described by Jarms & Tiemann (2004), jellyfish well exceeding the size of the oral disc of the sea anemone may be ingested as a result of a considerable inflation of its mouth and its oral disc. In shallow water this is exactly the same (see e.g. Ates 2002 and S. Daly in Wood 2013).

Predation upon jellyfish by decapod crabs is equally widespread (Table 1). None of the records seem to indicate that decapod crabs first attack the gonads, the most nutritious part of the jellyfish (cf. Rasmussen 1973). Contrary to sea anemones, decapod crabs may be able to actively pursue jellyfish as has been reported by Esser et al. (2004) for *Pagurus bernhardus* jumping up to capture *P. pileus* from the water column. Decapod crabs also are able to protect and defend their jellyfish prey, e.g. by moving away from a disturbance with it. This has been documented for *Callinectes sapidus* by Farr (1978) and for *Hyas araneus* by Ates & Hoyinck (2012). Farr (1978) suggested that crabs may only prey on jellyfish in the absence of other prey. However, I can testify that in the majority of cases witnessed by me (see Table 1) other prey items were available, sometimes abundantly. It is not easy to have decapod crabs accept a jellyfish prey in situ as they are easily disturbed by the presence of a diver contrary to sea anemones. In cases where such an experiment succeeds, most crab species grab and eat the jellyfish.

Echinoderms have rarely been mentioned as scavengers of jellyfish. There can however be no doubt that *Ophiocomina nigra* plays an important role as such (Ates & Hoyinck 2012). During three dives in Loch Sunart (Scotland) Ates & Hoyinck (2012) observed at least twelve dead specimens of *A. aurita* in various stages of consumption by *O. nigra* and to a lesser extent by *Asterias rubens* and *Ophiothrix gracilis*. The jellyfish was always consumed from the outside in, leaving the highest part of the velum to be eaten last. There is no indication that echinoderm scavengers go for the gonads first, if these are present.

As jellyfish often occur in swarms, their simultaneous death may lead to a high number of jellyfish carcasses raining down on the sea floor in a limited period of time at certain locations. In the last decade this has led to an increased interest in the impact of jellyfish carcasses on deep-sea ecology (e.g. Lebrato et al. 2012). Yamamoto et al. (2008) implicated one sea anemone, two decapod, one gastropod and one ophiurid species to be scavengers of *Nemopilema nomurai* carcasses in deep water of the Sea of Japan. In their experiments in a deep Norwegian fiord Sweetman et al. (2014) found evidence of scavenging by hagfish and some species of small crustaceans in high numbers consuming jellyfish carcasses in a matter of hours. If a high number of dead jellyfish fall down in a very short time scavengers may be too few to deal with their remains, as has been documented by Billett et al. (2006) and Lebrato et al. (2012). Billett et al. (2006) did not investigate the diet of the spider crab *Encephaloides armstrongi* Woodmason present in large numbers as can be seen on their picture 3A. Elsewhere spider crabs are known as predators or scavengers of jellyfish, see Table 1.

Incidentally some of the records of predation on jellyfish mentioned in the introduction relate to non-pelagic fishes. Luttenberger (1981), Chaves et al. (2010), Thaler (2012) and Dias & Almeida (2015) reported about coral reef fishes (e.g. species of *Chaetodon, Zebrasoma, Pomacanthus* and *Naso*) in different parts of the world benefitting from the influx of jellyfish into their realm. All these authors described the events as feeding frenzies, leading to the (near-)annihilation of the jellyfishes. This and my list of benthic invertebrate predators and scavengers (Table 1) contradicts the notion that "jellyfish are not readily consumed by other predators" (Condon et al. 2011). Quite the opposite may occur when jellyfish hit the coast or the sea floor. No barrier seems to exist for many benthic animals to consume dead or live jellyfish with relish. I have no doubt that proper fieldwork will reveal that jellyfish are being consumed by many more benthic scavengers and predators other than those contained in Table 1.

Plate 1.

A. *Cerianthus lloydii* (Cnidaria: Anthozoa: Ceriantharia) engulfing *Neoturris* cf *pileata* measuring less than 1.5 cm in diameter. Depth about 7 m. Picture taken on June 27, 2012 on the Lochaline Wall (Sound of Mull, Scotland) by R. M. L. Ates.

B. A young *Aurelia aurita* measuring about 3 cm in diameter being taken by an immature *Metridium senile* in Dutch coastal waters. Depth unknown. Picture taken by R. Offermans on April 9, 2011.

C. Two *Sagartia elegans* holding one *Chrysaora hysoscella*. Diameter of the sea anemones between 3 and 4 cm. Depth about 5 m. Picture taken by R. Offermans in the Oosterschelde estuary, southwestern Netherlands on July 17, 2015.

D. *Sagartiogeton undatus* caught in the act of engulfing *Aequorea vitrina*, diameter about 5 cm. Depth about 10 m. Picture taken by R. M. L. Ates in July, 2005 in the Grevelingen, southwestern Netherlands.

E. Unknown sea anemone consuming *Mastigias* sp. in Lake Kakaban, Kalimantan, Indonesia. Column height of the sea anemone about 5 cm. Depth unknown. Picture taken on October 2, 2010. Courtesy H. van Rijn.

F. *Necora puber* eating *Cyanea lamarckii*, diameter less than 10 cm. Depth about 7 m. Picture taken in the Oosterschelde, Netherlands in August 2003 by R. M. L. Ates.

G. Large numbers of *Pelagia noctiluca* may perish after entering Mgar-Ix-Ieni, Gozo, Malta due to southern winds. Their carcasses, less than 5 cm in length, are consumed by e.g. *Pagurus anachoretus.* Depth about 12 m. Picture taken in October 2002 by R. M. L. Ates.

H. This mature *Pagurus bernhardus* is halfway through processing an *Aurelia aurita*. Depth about 3 m. Picture taken in June 2003 in Loch Fyne, Scotland by R. M. L. Ates.

In her discussion Arai (2005) expressed the hope that awareness of the predation on jellyfish would lead to more knowledge of their role in pelagic food webs. Likewise I express the hope that this awareness will be extended to the benthic domain where many potential predators and scavengers await live or dead jellyfish coming within their reaches.

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