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, Suzao 2008, Cardona et al. 2013, 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, Eatonina, Euchaeilota 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 anenomes 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* lamarkii 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 (Romane, 1876) | Oosterschelde, Netherlands | Cargo & Schultz 1967*; Cones & Haven 1969 |
| Diadumene leucolea (Verrill, 1866) | *Chrysaora quinquecirrha* (DeSor, 1848) | western Atlantic | pers. comm. M. Vestjens 2002 |
| Metridium farcimen (Brandt, 1835) | *Cyanea capillata* (Linnaeus, 1758) | northeastern Pacific | pers. comm. R. Harbo 2012 |
| Metridium senile (Linnaeus, 1767) | Pileus | northeastern Pacific | pers. comm. C.E. Mills 2000 |
| Metridium senile | hydroid fragments | Grevelingen, Netherlands | Ates 2002 |
| Metridium senile | *A. aurita, P. pileus, Chrysaora hysoscella* | Oosterschelde, Netherlands | this paper, see photo B |
| Metridium senile | *A. aurita* | northeast Atlantic | Sebens & Kochl 1984 |
| Metridium senile | jellyfish | Grevelingen, Netherlands | Ates 2002 |
| Paraphellactis pabista Dunn, 1982 | jellyfish | Aequorea victoria (Murbach & Shearer, 1902) | this paper, see photo C |
| Sagartia sp. | *P. pileus* | western Atlantic | pers. obs. July 2007 |
| Sagartia elegans (Dalyell, 1848) | *C. hysoscella* | Grevelingen, Netherlands | pers. comm. P. Lovejoy Sept. 2000 |
| Sagartia troglodytes (Price in Johnston, 1847) | *A. aurita, C. hysoscella* | Oosterschelde, Netherlands | Ates 2014 |
| S. troglodytes | *E. indicans* | Oosterschelde, Netherlands | Ates 2014 |
| Sagartiogeton lacertus (Dalyell, 1848) | *A. aurita* | North Sea | Berryman 1984 |
| Sagartiogeton undatus (Müller, 1778) | *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* | North Sea | Ates 2014 |
| 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. 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) | *Echinostoma pulmo* | 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 | Hocksema et al. 2014 |
| sea anenome | *M. papua* | Palau, western Pacific | Hamner 1982 |
| sea anemone | *E. (?) medusivora* | Palau, western Pacific | Hamner & Hauri 1981; Fautin & Fitt 1991 |
| sea anemone | *A. aurita ephypae* | Waddenzee, Netherlands | Swennen 1996* |
| sea anemone | *Nemopilema nomurai* Kishinouye, 1922 | Sea of Japan | Yamamoto et al. 2008 |
| **Cnidaria other than Actiniaria** | | | |
| *Aiptasia pulchella* (?) | *P. pileus* | | |
| Cerianthus lloydii Gosse, 1859 | cf. *Neoturris pileata* | Scottish waters | this paper, see photo A |
| Fungia scarpousa Klunzinger, 1879 | *A. aurita* | Red Sea | Alamaru et al. 2009 |
| Tubulularia sp. | Lensia sp. | ? | Mackie 1966 |
| Tubulularia larynx Ellis & Solander, 1876 | gelatinous plankton | Irish Sea | Gili et al. 1996 |
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| 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, 1907) | 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 |
| Hya subaraneus (Linnaeus, 1758) | C. capillata | Scottish waters | Ates & Hoyinek 2012 |
| H. araneus | A. aurita | Scottish waters | pers. comm. W. Northway May 2011 |
| Jasus lalandii (Milne-Edwards, 1837) | hydrodusae | ? | Williamson, in Thomas 1963* |
| Leiocarcinus depurator (Linnaeus, 1758) | C. capillata | Scottish waters | pers. comm. W. Northway Sept 2013 |
| Menippe mercenaria (Say, 1818) | Stomolophus | Gulf of Mexico | Powell & Gunter 1968 |
| Nucella lapillus (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 quadrida (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 & Hoyinek 2012; this paper, see photo H |
| Pagurus floridanus (Benedict, 1892), Pagurus parallelus Say, 1817 | Cyanea, Stomolophus | Gulf of Mexico | Phillips et al. 1969* |
| Portunus holsatus Fabricius, 1798 | P. pileus | North Sea | Greve 1972* |
| Plesiopeanu 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 tenuimanus 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 & Hoyinek 2012 |
| Ophiocomina nigra (Abildgaard, 1789) | A. aurita | Scottish waters | Ates & Hoyinek 2012 |
| Ophiuroidea fragils (Abildgaard, 1789) | A. aurita | Oosterschelde, Netherlands | Ates 2002 |
| O. fragils | A. aurita | Scottish waters | Ates & Hoyinek 2012 |
| seastar (Anseropoda ?) | jellyfish | California | Wu 1998 |
| Stronglyocentrotus 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
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 Ophiophris 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. Sagartiotogen undatus caught in the act of engulfing Aequorea viritina, 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 lamarekii, 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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