Non-size-selective predation on fish larvae by moon jellyfish *Aurelia aurita* under low oxygen concentrations

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Received 16 December 2006; Accepted 21 October 2007

**Abstract:** The moon jellyfish *Aurelia aurita* has increased in abundance in coastal waters around Japan during recent decades. Since the moon jellyfish is highly tolerant of low dissolved oxygen concentrations, predation impacts by moon jellyfish on zooplankton can increase during summer hypoxia in coastal waters, which is often caused by anthropogenic effects such as an increase in nutritional loading from the land. Laboratory experiments were conducted in order to test the hypothesis that summer hypoxia leads to qualitative changes in predator-prey interactions between moon jellyfish and larval fish. Larvae of a common coastal fish, red sea bream *Pagrus major* (2.9, 4.1, 6.2 and 8.6 mm in standard length), were used for the experiments. Predation rates (% of larvae preayed on by a moon jellyfish per 10 min.) were examined at four oxygen concentrations (1, 2, 4 and 5.8 mg L\(^{-1}\)) in 10 L tanks (4 replicates). Size-selective predation was observed at the two highest oxygen concentrations (4 and 5.8 mg L\(^{-1}\)): about half of the 6.2 and 8.6 mm larvae survived the 10 min. trials while more than 85% of the 2.9 and 4.1 mm larvae were captured. Larval body size did not affect the predation rates at the two lowest oxygen concentrations (1 and 2 mg L\(^{-1}\)): more than 90% of larvae in all size classes were caught. These results indicate that trophic flow from ichthyoplankton to moon jellyfish increases during summer hypoxia in coastal waters and a qualitative change in predator-prey interaction, i.e., shift from size-selective to non-size-selective predation occurs at oxygen concentrations <2 mg L\(^{-1}\).

**Key words:** fish larvae, hypoxia, moon jellyfish, predation, predator-prey interactions

**Introduction**

Abundances of large gelatinous zooplankton such as cnidarians and ctenophores are reported to have increased in many marine systems around the world (Purcell & Arai 2001, Brodeur et al. 2002). Gelatinous zooplankton constitutes a significant part of the total predator population in coastal and estuarine plankton communities (Uye & Ueta 2004). Increases in gelatinous zooplankton abundances have the potential to alter the balance of trophic pathways between smaller zooplankton and their predators in marine ecosystems.

The moon jellyfish *Aurelia aurita* (Linnaeus 1758) is widely distributed throughout the coastal waters of the world. The biomass of moon jellyfish is reported to have increased over recent decades in Tokyo Bay (Toyokawa et al. 2000, Ishii 2001) and in the Seto Inland Sea (Uye & Ueta 2004). Moon jellyfish are considered to be important predators of fish larvae as well as other invertebrate plankton (Bailey & Batty 1984, Sullivan et al. 1994). Möller (1984) observed 68 Atlantic herring *Clupea harengus* (Linnaeus 1758) larvae were eaten by a single moon jellyfish (42 mm in bell diameter: BD) in Kiel Fjord. Recent laboratory experiments reported that more than 110 red sea bream *Pagrus major* (Temminck et Schlegel 1844) larvae were preyed on by a moon jellyfish (66–80 mm BD) during a short-term satiation experiment (Nakayama et al. 2003). Increases in moon jellyfish biomass in the coastal waters of Japan would lead to higher mortality of coastal fish larvae due to predation.

In the Seto Inland Sea, excess nutritional loading from the land exacerbates the depletion of oxygen concentration during summer (Okaichi et al. 1996). Dissolved oxygen concentration commonly declines to <1 mg L\(^{-1}\) during summer in several bays and inner parts of the Seto Inland Sea. Low oxygen concentrations in stratified water can lead to lethal effects on benthic and pelagic organisms (Officer et al. 1984, Aoki 1999). Declines in dissolved oxygen to moderate levels of hypoxia (ca. 1–2 mg L\(^{-1}\)), which is not lethal during a short-term exposure, can reduce larval ability to escape from predators and increase mortality due to predation (Breitburg et al. 1994, Shoji et al. 2005a).
Recent laboratory experiments reported that bell contraction rate and predation rate on fish larvae (<5 mm in standard length) by moon jellyfish under oxygen concentrations <2 mg L⁻¹ were similar to those under higher oxygen concentrations (4–6 mg L⁻¹: Shoji et al. 2005b). These observations show that moon jellyfish of the genus *Aurelia* are highly tolerant to low oxygen concentrations, as are several other jellyfish species (Breitburg et al. 1994, Keister et al. 2000, Thuesen et al. 2005) and indicates that the relative importance of trophic flow from fish larvae to moon jellyfish may increase due to changes in predator-prey interactions during summer hypoxia in coastal waters.

Qualitative evaluations, in addition to quantitative evaluations, will be indispensable for integrated analysis of predator-prey interactions between moon jellyfish and fish larvae and spatio-temporal changes in the interactions. Generally, larger fish larvae are more able to escape from predators because of their higher swimming ability and this results in 'size-selective' predation (Bailey & Houde 1989). On the contrary, the vulnerability of larger larvae to predation by moon jellyfish increases under hypoxic conditions since swimming performance of fish larvae decreases under low oxygen concentrations (Breitburg et al. 1994, Shoji et al. 2005a), and this may result in 'non-size-selective' predation. In the previous studies, however, most attention was paid to quantitative analysis of predator-prey interactions between jellyfish and fish larvae (e.g. how dissolved oxygen affects predation/survival rates of fish larvae in the same size class: Breitburg et al. 1994, Shoji et al. 2005b).

In the present study, laboratory experiments were conducted in order to test the hypothesis that a qualitative change in predator-prey interactions between moon jellyfish and fish larvae, in particular, shift from size-selective to non-size-selective predation, occurs when oxygen concentration declines to moderate levels of hypoxia. Red sea bream *Pagrus major* larvae were used as prey in the predation experiments. The red sea bream is widely distributed and is one of the most important fisheries resources in the southwest coastal and inland waters of Japan. Pelagic larvae and juveniles are abundant from March to May in Shijiki Bay (Tanaka 1980) and in May and June in the Sea of Hichichi, central waters of the Seto Inland Sea (Shoji et al. 2002). Late larvae and early juveniles migrate from coastal open waters to settle in the shallow waters of bays in May and June (Azeta et al. 1980).

**Materials and Methods**

Moon jellyfish were collected with a 10-L plastic bucket at the pier of the Maizuru Fisheries Research Station (MFRS), Center for Education and Research of Field Science, Kyoto University, and were kept in 100-L tanks with aerated seawater. The moon jellyfish were fed with *Artemia* spp. Water temperature ranged between 19.0–21.6°C.

**Results**

In order to detect the effect of oxygen concentrations and prey body size on the predation rate of the moon jellyfish, experiments were conducted at four oxygen concentrations (1.0±0.1, 2.0±0.1 and 4.0±0.1 mg L⁻¹ and air saturated: 5.8±0.2 mg L⁻¹) with four body length classes of red sea bream larvae (2.91±0.04, 4.07±0.11, 6.19±0.18 and 8.60±0.15 mm). As a result, 16 combinations (4 replicates for each) were designed for the predation experiments. Water temperature ranged between 19.1–21.5°C during the experiments. The desired oxygen concentrations were obtained by bubbling filtered seawater with nitrogen and air. Oxygen concentrations within ±8% of the desired concentration were obtained. Each 10-L experimental tank was sealed after 30 red sea bream larvae and one moon jellyfish were introduced. The number of larvae preyed on by the moon jellyfish during a 15-min. time period was counted and the bell diameter of the moon jellyfish was measured at the end of each experiment. The predators were not reused.

**Discussion**

Results of the present experiments demonstrate that a qualitative change in predator-prey interactions between jellyfish and fish larvae occurs under moderate levels of hypoxia. Predation on the larvae by the moon jellyfish was size-selective at the two highest oxygen concentrations (4 and 5.8 mg L⁻¹) while it became non-size-selective at the two lowest oxygen concentrations (1 and 2 mg L⁻¹).

Vulnerability of fish larvae to predators is affected by the predator:prey size ratio (Bailey & Houde 1989). The lower predation rates on larger fish larvae by moon jellyfish at the
higher oxygen concentrations examined in the present study suggest that the larger fish larvae were more able to avoid predation by the moon jellyfish. Swimming speed has been reported to rapidly increase in red sea bream larvae greater than 6 mm in standard length under laboratory conditions (Fukuhara 1985). Time elapsed before capture by a moon jellyfish significantly increased in red sea bream larvae greater than 7 mm (Nakayama et al. 2003). These observations support the conclusion that the larger red sea bream larvae (6.2 and 8.6 mm) were more able to escape moon jellyfish predation than the smaller larvae (2.9 and 4.1 mm). Therefore, size-selective predation prevailed at the two highest oxygen concentrations (Fig. 2).

The similar predation rates (ca. 90%) on larvae of all size classes that was observed at the two lowest oxygen concentrations (1 and 2 mg L$^{-1}$) indicate the larger larvae (6.2 and 8.6 mm) were unable to escape from moon jellyfish as readily as they could at the two highest oxygen concentrations (4 and 5.8 mg L$^{-1}$). Oxygen concentrations <2 mg L$^{-1}$, which commonly occur during summer in the coastal waters of Japan, may not be lethal to red sea bream larvae when exposure time is short. However, these oxygen concentrations constitute a moderate level of hypoxia and are considered to be physiologically stressful to larval fish and to reduce the ability of larvae to escape from predators (Rombough 1988). It is likely that the difference in tolerance to low oxygen concentrations between the moon jellyfish and red sea bream larvae changed the nature of the predator-prey interaction and resulted in non-size-selective predation at 1 and 2 mg L$^{-1}$ (Fig. 2).

It is concluded that a qualitative change in predator-prey interactions between moon jellyfish and fish larvae occurs at moderate levels of hypoxia under laboratory conditions. Non-size-selective predation became more common when oxygen concentration decreased to about 2 mg L$^{-1}$. Since the moon jellyfish is highly tolerant to low dissolved oxygen concentrations, both quantitative and qualitative changes in predator-prey interactions may occur in coastal waters during summer hypoxia caused by anthropogenic effects such as an increase in nutritional loading from the land.

**Acknowledgements**

The author expresses sincere thanks to Dr. Yoh Yamashita, Dr. Reiji Masuda and staff of MFRS, Kyoto University, for providing the rearing facility and Dr. Hiroshi Motoh and staff of KPSFC for providing red sea bream eggs. This paper was presented at the Topic Session on “The human dimension of jellyfish blooms” convened at the PICES Fifteenth Annual Meeting in Yokohama, Japan, October 2006.
References


