1 Behavioural responses of zooplankton to the presence of predatory jellyfish

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15 **Abstract**

16 The major objective of this study was to investigate the behavioural responses of several
17 zooplankton species to the presence of the scyphozoan jellyfish, Catostylus mosaicus. Specific aims
18 included: identifying taxa that were not captured by C. mosaicus; investigating whether some of
19 these taxa were able to detect and avoid water that had been exposed to C. mosaicus; and
20 determining if the vertical movement of crab megalopae was suppressed in the presence of C.
21 mosaicus. Zooplankton not caught by C. mosaicus were identified by comparing the zooplankton
22 present in the water column to those on the oral arms of the jellyfish. C. mosaicus mainly caught
23 mollusc veligers and copepods, but did not catch crab megalopae, small prawns or post-flexion fish
24 larvae. The hypothesis that these taxa were able to avoid swimming in water exposed to C. mosaicus
25 was tested using water-choice experiments in a flume tank. A significant proportion (18 – 25 %) of
26 larval barramundi (Lates calcarifer) avoided swimming in the plume of water that had been exposed
27 to C. mosaicus but mud crab (Scylla serrata) megalopae and juvenile prawns showed no response.
28 The effect of C. mosaicus on the vertical movement of S. serrata megalopae was tested using 1 m tall
29 glass towers. Megalopae were exposed to one of four treatments: filtered seawater (a control), an
30 oral arm of C. mosaicus, an oral arm that had been sealed in plastic, and mucus from C. mosaicus.
31 Megalopae migrated higher into the water column in the control than in treatments containing cues
32 from the jellyfish. These findings suggest that blooms of jellyfish may induce behavioural changes
33 in some zooplankton.

34

35 Keywords: Catostylus mosaicus, Scyphozoa, fish larvae, crab megalopae, predator avoidance,
36 vertical migration, flume tank

37 **Introduction**

38 Predation by jellyfish on zooplankton (Purcell, 1992; Brodeur et al., 2002; Graham et al., 2003) and
39 the competition exerted by jellyfish on other zooplanktivores (Purcell and Sturdevant, 2001; Brodeur
40 et al., 2002) are the two most well-recognised ways gelatinous predators impact pelagic
41 assemblages. Since there is compelling evidence that jellyfish blooms have increased in some parts
42 of the world (Brodeur et al., 1999; Link and Ford, 2006; Lynam et al., 2006), there is a growing need
43 to identify other means by which pelagic communities are impacted by jellyfish.

44
45 Jellyfish capture only some of the zooplankton taxa present in the water column (e.g. Purcell and
46 Arai, 2001; Peach and Pitt, 2005). Selectivity may occur due to structural differences in the
47 nematocysts of medusae that favour capture of particular types of prey (Purcell and Mills, 1988).
48 Nematocysts may also be discharged selectively in response to chemical stimuli released from
49 particular zooplankton (Purcell and Anderson, 1995) and post-capture sorting by the jellyfish can
50 further influence which zooplankton are retained (Arai, 1997). The sensory and locomotory abilities
51 of zooplankton, however, may also influence their likelihood of capture. Some zooplankton with
52 well-developed locomotory abilities may be able to escape medusae after initial capture (Purcell,
53 1985; Arai, 1997), while others may be able to detect and actively avoid medusae altogether. The
54 ability of zooplankton to detect medusae and alter their behaviour to avoid capture is poorly known.

55
56 Some zooplankton alter their behaviour in the presence of predators. For example, predatory fish can
57 induce vertical migration in freshwater Daphnia (Van Gool and Ringelberg, 1998), or alter the extent
58 of the migration of marine copepods (Hays, 1994; Kornilovs et al., 2001) and crab larvae (Forward
59 and Rittschof, 2000). Cohen and Forward (2003) have provided one of few examples of the effect of
60 gelatinous predators on zooplankton behaviour. They showed that the shadows of the ctenophore

61 Mnemiopsis leidyi, and the chemical cues (kairomones) released from the ctenophore's mucus,
62 caused zoea of the crab, Rhithropanopeus harrisii, to descend in the water column.

63

64 Catostylus mosaicus (Scyphozoa; Rhizostomeae) (Quoy and Gaimard, 1824) is a large medusa
65 (>150 mm bell diameter (BD)) that frequently forms spectacular blooms in the estuaries and coastal
66 waters of eastern Australia (Pitt and Kingsford, 2000). During blooms, average concentrations of
67 adult medusae can exceed 1 m^{-3} (Pitt and Kingsford, 2003) and in localised patches, small medusae
68 may exceed 1000 m^{-3} (Kingsford et al., 2000). C. mosaicus primarily captures mollusc veligers,
69 copepods and copepod nauplii (Browne and Kingsford, 2005; Peach and Pitt, 2005) but captures few
70 other gelatinous zooplankton, or the later developmental stages of meroplankton, including post-
71 flexion fish larvae and crab megalopae (Browne and Kingsford, 2005; Peach and Pitt, 2005),
72 suggesting that these animals are either selected against, can escape once caught, or actively avoid
73 capture. While swimming, C. mosaicus is often observed to release strands of mucus (Pitt, pers.
74 obs.) which may contain chemicals that act as a cue to the zooplankton about the presence of
75 medusae.

76

77 The major objective of this study was to investigate the behavioural responses of zooplankton to the
78 presence of C. mosaicus. Specific aims were to: 1) compare the assemblages of zooplankton
79 captured by C. mosaicus to the assemblages available for capture in the water column to identify
80 zooplankton that may actively avoid capture; 2) discover, using water-choice experiments in a flume
81 tank, whether some zooplankton not captured by C. mosaicus avoided water that contained
82 chemicals derived from the jellyfish; and 3) determine if the vertical movement of crab megalopae
83 was inhibited by the presence of C. mosaicus.

84

85 **Methods**

86 **Comparison of zooplankton on the oral arms of Catostylus mosaicus and in the water column**

87 Assemblages of zooplankton in the water column and on the oral arms of C. mosaicus were sampled
88 on four occasions (August 8, October 7, November 13 and 23, 2005) in Moreton Bay, Queensland,
89 Australia (27°16' S, 153°15' E). On each occasion, samples were collected during the day and night
90 to account for diurnal differences in assemblages associated with nocturnal emergence of demersal
91 zooplankton from the benthos (Jacoby and Greenwood, 1989). Samples at night were collected a
92 minimum of three hours after sunset since scyphozoans digest most prey within 1 – 3 hours
93 (Båmstedt and Martinussen, 2000). A minimum of two and usually three sites, separated by > 1 km
94 and chosen based on the presence of C. mosaicus, were sampled.

95
96 At each site, three jellyfish (150 – 190 mm BD) were collected from within 1 m of the surface using
97 a dip net. The oral arms were detached from the bell and shaken vigorously in filtered (10 µm) sea
98 water for 90 seconds to remove the zooplankton (sensu Browne and Kingsford, 2005). As C.
99 mosaicus appears to predominantly occur (Pitt and Kingsford, 2003) and, therefore, feed close to the
100 surface, three samples of zooplankton were collected using a 100 µm plankton net that was hauled
101 vertically from a depth of 3 m. All samples were preserved in 3% formalin (final concentration). In
102 the laboratory, zooplankton were identified to the taxonomic resolution of at least class and, where
103 relevant, into different life-history stages. Taxa were enumerated by sorting two 25 mL sub-samples
104 (together accounting for approximately ¼ to ½ of the total sample). The remainder of each sample
105 was briefly inspected to ensure all zooplankton taxa had been accounted for.

106
107 Differences in assemblages of zooplankton present on the oral arms and in the water column were
108 analysed using multivariate techniques. Data were standardised to relative abundances to enable

109 meaningful comparisons between samples from the oral arms (i.e. numbers jellyfish⁻¹) and the water
 110 column (i.e. numbers m⁻³). Multidimensional scaling plots (MDS plots) based on Bray-Curtis
 111 similarity measures were used to graphically display differences between assemblages of
 112 zooplankton on the oral arms and in the water column during the day and night for each of the four
 113 times sampled. Separate one-way Analyses of Similarities (ANOSIMs) were used to test if
 114 differences were statistically significant. If ANOSIMs detected differences, Similarities of
 115 Percentages (SIMPERs) were used to identify which zooplankton groups contributed most to the
 116 dissimilarities between the samples.

117
 118 **Responses of zooplankton to the chemicals of Catostylus mosaicus in a flume tank**

119 Three zooplankton taxa (crab megalopae, post-flexion larval fish and juvenile penaeid prawns) that
 120 were present in the water column but not caught by C. mosaicus were tested in a flume tank for their
 121 ability to avoid water containing chemicals derived from C. mosaicus. Hatchery-reared crab and fish
 122 larvae were used for experiments as this was the only means by which sufficient quantities of
 123 animals at the same stage of ontogenetic development could be obtained. The crab megalopae were
 124 represented by intermolt (i.e. between several hours and 2 days into the megalopal stage) mud crab
 125 megalopae, Scylla serrata (Forskål), and post-flexion larval fish were represented by 10-13 day old
 126 barramundi larvae, Lates calcarifer (Bloch). Both zooplankters are commercially important species
 127 that co-occur with C. mosaicus (Dunstan, 1959; Heasman et al., 1985). The S. serrata megalopae
 128 were produced by one wild-caught female collected in Moreton Bay, and the larval L. calcarifer
 129 were produced by one wild-caught female collected in the Cairns/Innisfail region (D. Mann, BIARC,
 130 pers. comm.). Flume tank experiments were conducted at the Bribie Island Aquaculture Research
 131 Centre (BIARC), Queensland Department of Primary Industries and Fisheries, from 11-13
 132 November 2005 for S. serrata and 5-7 December 2005 for L. calcarifer. Since hatchery-reared

zooplankton may not respond to jellyfish in the same way as wild-caught zooplankton, experiments were repeated using juvenile (approximately 1cm) penaeid prawns caught using plankton tows and emergence traps at Smiths Lake, a coastal lagoon in New South Wales (32°22' S, 152°27' E). Given that the wild-caught prawns would have been produced by multiple females, this experiment also eliminated possible artefacts that may have been introduced in the previous experiments by using test animals that had been derived from a single wild-caught female. Experiments were undertaken at Smiths Lake from 7-9 February 2006.

The flume tank was made of clear Perspex, had the dimensions 5 x 40 x 120 cm (H x W x L), and was modelled on that used by Atema et al. (2002). Two sources of water were introduced at the front of the tank and were initially separated by a Perspex divider. Each source of water flowed through packed straws (to create laminar flow), then entered a common chamber (40 x 40 cm) and was released through outlets at the rear of the tank. 0.5 mm mesh was placed at the front and rear of the common chamber to retain the test animals within this area. The two sources of water remained separated by a distinct interface in the common chamber, which the test animals could cross at will.

Flow rates were adjusted to ensure that the test animals could swim without obvious exertion or distress (approximately 5 cm s⁻¹). Food dye was used to measure rates of flow and to ensure the two sources of water remained separated within the common chamber. Water was pumped into the flume tank from two 300 L tanks. One tank contained filtered seawater and the other held filtered seawater that been exposed to C. mosaicus, henceforth termed jellyfish water. The seawater at BIARC was pumped from the eastern (ocean) side of Bribie Island. The inlet was located 100 m from shore at a depth of approximately eight metres (D. Mann, BIARC, pers. comm.). Jellyfish were not abundant on the eastern side of the island so the water was unlikely to have contained chemicals associated

with C. mosaicus. The seawater flowed through a vertically stratified sand bed and was filtered to approximately 20 μm (D. Mann, BIARC, pers. comm.). Jellyfish were captured daily from the Pumicestone Passage on the south-western side of Bribie Island. Jellyfish water was created by placing one C. mosaicus (150 – 190 mm BD) in a 300 L tub of filtered seawater. The jellyfish actively swam about the tub and produced mucus. After one hour the jellyfish was removed and the water was filtered through 10 μm and 1 μm nosebag filters to remove mucus and nematocysts (Peach and Pitt, 2005).

The study consisted of three treatments: a control, where filtered seawater flowed through both sides of the tank; and two jellyfish treatments, referred to as FJ and JF. In FJ, filtered seawater (F) flowed through the left side of the tank and jellyfish water (J) flowed through the right, and in JF the order was reversed. The control ensured the zooplankton displayed no preference for a particular side of the tank and identified whether their behaviour changed over the duration of the experiment. The FJ and JF treatments were used to determine if the zooplankton avoided the jellyfish water.

Ten zooplankton were added to the common chamber in non-flowing filtered seawater for 30 minutes to acclimate to the flume tank. Flowing filtered seawater was then introduced into both sides of the tank for ten minutes (Flow Acclimation period), after which jellyfish water was introduced into the appropriate side of the tank in the FJ and JF treatments (Treatment Flow period). The Treatment Flow ran for 18 minutes. The number of animals on each side of the tank was recorded at one minute intervals during the last three minutes of the Flow Acclimation and Treatment Flow periods and the average number on each side was calculated for each period.

Experiments using crab megalopae and fish larvae were each repeated four times, with the order of treatments interspersed. All experiments were done during the day, indoors, and the flume tank was flushed with filtered seawater between experiments. When testing the response of juvenile penaeid prawns at Smiths Lake, variations to the experimental procedure were made due to reduced access to running seawater. Specifically, each treatment was repeated only three times; jellyfish water was produced by housing one jellyfish in a 100 L tank for 20 minutes; the Flow Acclimation period was reduced to 5 minutes; and the Treatment Flow was reduced to 8 minutes. Different test animals were used for each experiment to ensure independence.

A one-way ANOVA found no difference among treatments (control, FJ and JF) in the average number of any zooplankton species in the left side of the tank during the Flow Acclimation period ($P > 0.05$). Furthermore, the zooplankton were evenly distributed across each side of the tank. Therefore, the difference in the number of zooplankton in the left side of the tank between the Flow Acclimation and Treatment Flow periods was used as the dependent variable to test the response of zooplankton to the jellyfish water. Differences in the response of zooplankton among the three treatments were tested for each species using a one-way ANOVA. Our hypothesis was considered to be supported if numbers of zooplankton in the left side of the tank decreased in the JF treatment, increased in the FJ treatment and remained similar in the control treatment. For all ANOVAs the assumption of homogeneity of variances was tested using a Cochran's test and, if differences were detected, post-hoc Student Newman Keuls (SNK) tests were used to identify where differences occurred.

202 **The influence of Catostylus mosaicus on the vertical movement of Scylla serrata megalopae**

203 The effect of jellyfish on the vertical movement of hatchery-reared S. serrata megalopae was tested
204 from 11-13 November 2005, at BIARC. The experiment used 12 glass towers (100 x 10 x 9 cm; H x
205 W x L; sensu Webley and Connolly, 2007) to observe the vertical movement of the megalopae on a
206 small scale. The towers were positioned in two rows of six, aligned back to back. Three vertical
207 faces of each tower were covered in black adhesive to prevent megalopae in adjacent towers from
208 seeing each other and to minimise disturbance by external stimuli. A fluorescent light was positioned
209 lengthwise over the centre of the block of towers and was used to stimulate vertical migration (sensu
210 Webley and Connolly, 2007). The experiment was repeated three times during the day and night,
211 with the day and night experiments interspersed over the three days. The use of the fluorescent light
212 in the night experiments was not intended to mimic natural levels of irradiance, but to provide
213 standard test conditions to detect whether the response of the megalopae to cues from the jellyfish
214 would differ between the day and night due to possible circadian rhythms.

215

216 Towers were filled with filtered seawater and sand was placed in the bottom of each tower to prevent
217 reflection of light. The experiment consisted of four treatments. Towers in the control treatment
218 contained only filtered seawater. In the second treatment an oral arm from a recently-caught C.
219 mosaicus was suspended at the surface (whole jellyfish were not used because the rhythmic
220 contractions of their bells could influence the vertical position of the megalopae). The third
221 treatment contained an oral arm that was sealed within multiple layers of plastic cling film and
222 suspended at the surface of each tower. This treatment provided a similar visual cue to the oral arm
223 treatment but did not release any chemicals. In the final treatment mucus that had been produced by
224 a jellyfish was floated at the surface of each tower. The mucus treatment contained the same

chemicals as the oral arm treatment, but a much reduced visual cue. Each treatment was randomly allocated to three towers and towers were randomly repositioned for each experiment.

Ten megalopae were added to each tower and acclimated for two hours in darkness. During acclimation megalopae remained close to the bottom of the towers (a dim, incandescent torch, covered with red cellophane was used to check the positions of the megalopae in darkness, sensu Webley and Connolly, 2007). The treatments were established and vertical movement was initiated by switching on the fluorescent light. After being exposed to light for two hours, the vertical position (0 cm – bottom to 100 cm – top) of each megalopa was recorded and the average height of megalopae in each tower was used as the dependent variable.

Differences in the vertical positions of crab megalopae were analysed using a three-way ANOVA. The factors were time (a fixed, orthogonal factor with two levels: day and night); experiment (a random factor, nested within time); and treatment (a fixed orthogonal factor with four levels: control, oral arm, sealed oral arm and mucus).

Results

Comparison of zooplankton assemblages on the oral arms and in the water column

On all occasions, C. mosaicus caught approximately 50% of the zooplankton taxa that were present in the water column (Table 1). Gastropod and bivalve veligers, copepods, brachyuran crab zoea and amphipods were the most abundant taxa on the oral arms of C. mosaicus. Numerous zooplankton, including ostracods and barnacle nauplii, were present in the water column but did not occur on the oral arms. C. mosaicus caught the early developmental stages of several taxa including crab zoea and pre-flexion larval fish, but did not capture the later developmental stages of these groups, despite

their presence in the water column. Gammarid amphipods were occasionally more prevalent on the oral arms of C. mosaicus than in the water column (Table 1). This may reflect a commensal association between the amphipods and C. mosaicus (*sensu* Browne and Kingsford, 2005).

MDS plots indicated that there were consistent differences in the assemblages of zooplankton in the water column and on the oral arms of C. mosaicus during both the day and night (Fig. 1) and ANOSIMs showed that these differences were statistically significant ($R > 0.93$; $P < 0.01$ in all cases). SIMPER identified calanoid, cyclopoid and harpacticoid copepods, and copepod nauplii, as the groups that consistently contributed most to the differences between zooplankton assemblages in the water column and on the oral arms, even though these organisms were present in both sample types.

Response of zooplankton to the chemicals of Catostylus mosaicus in the flume tank

The behaviour of the S. serrata megalopae and the juvenile penaeid prawns in the flume tank was similar. During the Flow Acclimation and Treatment Flow periods, individuals of both species alternated between remaining relatively stationary and swimming back and forth across the interface of the two water sources. The numbers of S. serrata megalopae and juvenile prawns on the left side of the tank, however, did not vary between the Flow Acclimation and Treatment Flow periods in any of the experimental treatments ($P > 0.05$ for both species) indicating no net movement by either species towards or away from the jellyfish water (Fig. 2).

Larval L. calcarifer frequently moved between the two sides of the flume tank but at the end of the experiments they showed a net movement away from the jellyfish water ($P < 0.01$). Specifically, the average number of L. calcarifer on the left side of the tank increased by 18% between the Flow

273 Acclimation and Treatment Flow periods in the FJ treatment; decreased by 25% in the JF treatment
 274 and remained similar in the control treatment (Fig. 2).

275

276 **Influence of Catostylus mosaicus on the vertical movement of Scylla serrata megalopae**

277 The heights to which the megalopae swam in the towers varied among the four treatments and the
 278 pattern of variation was the same in five of the six experiments ($P < 0.05$, Table 2). A post-hoc SNK
 279 test revealed that, for five experiments the megalopae moved significantly higher in the control
 280 treatment than in the three jellyfish treatments (Fig. 3A, B). In one experiment the heights of the
 281 megalopae in the control and sealed oral arm treatments did not differ, although megalopae in the
 282 mucus and oral arm treatments were lower than in the control (Fig. 3B). During all experiments,
 283 megalopae in the three jellyfish treatments remained below 25 cm, indicating that vertical movement
 284 of the megalopae was inhibited in each of these treatments.

285

286 **Discussion**

287 The major objective of this study was to identify which taxa were not caught by C. mosaicus and to
 288 determine whether some of these taxa altered their behaviour in the presence of the medusae. We
 289 observed that several groups of zooplankton did not appear on the oral arms of C. mosaicus, despite
 290 being reasonably abundant in the water column. Several of these groups, such as relatively slow
 291 moving echinoderm larvae (Chia et al., 1984), would presumably be easily caught by the medusae.
 292 For such zooplankton, their absence on the oral arms is likely to be a result of selectivity by the
 293 medusae, through mechanisms such as selective discharging of nematocysts or post-capture sorting
 294 (Purcell and Anderson, 1995; Arai, 1997). The absence of some of the more active zooplankton,
 295 such as ascidian larvae and barnacle nauplii (Chia et al., 1984), however, may reflect the ability of
 296 these zooplankton to escape after initial contact or to detect and avoid the medusae altogether.

297 Indeed, there was a strong indication that the ability to avoid capture may be related to the
298 ontogenetic development of some taxa. For example, larval polychaetes and the early developmental
299 stages of several meroplankton taxa were captured, but adult polychaetes and post-flexion larval fish
300 and crab megalopae were not. The ability of older fish larvae to evade capture by scyphozoans is
301 well known and is usually attributed to the increased sensory and locomotory abilities of the more
302 developed larvae (e.g. Bailey, 1984; Fancett, 1988).

303

304 Since no crab megalopae, late developmental stage fish larvae or juvenile prawns were found on the
305 oral arms of C. mosaicus in Moreton Bay, it was hypothesised that these groups may evade capture
306 by detecting and avoiding water containing chemicals of the jellyfish. Neither the juvenile penaeid
307 prawns nor the S. serrata megalopae responded to the jellyfish water in the flume tank, suggesting
308 that either they could not detect the chemicals of the jellyfish or, if they could detect them, they did
309 not respond to them. Cohen and Forward (2003) demonstrated that while chemicals from the
310 ctenophore, Mnemiopsis leidyi, were not the primary cues for avoidance by zoea of the crab,
311 Rhithropanopeus harrisi, the response to shadows from the ctenophore was heightened when the
312 chemical cues were present. This suggests that multiple cues from a predator may be required to
313 elicit a behavioural response in some zooplankton.

314

315 In contrast to the crustaceans, a significant proportion of larval L. calcarifer avoided water that had
316 been exposed to C. mosaicus. The ability to detect and respond to the kairomones of predators
317 appears to be widespread in aquatic environments (reviewed by Kats and Dill, 1998) and juvenile
318 and adult fish from freshwater systems can modify their behaviour when exposed to the kairomones
319 of predatory fish (Bryer et al., 2001; Mikheev et al., 2006). While the olfactory system of L.
320 calcarifer has not been studied, olfaction is well-developed in late-stage larvae of coral reef fish and

these fish can detect and respond to changes in water chemistry (Atema et al., 2002; Arvedlund and Takemura, 2006; Gerlach et al., 2007). Our data suggests that larval fish also may use chemosensory mechanisms to detect predatory jellyfish.

To ensure rigorous experiments, it was important that zooplankton at the same stage of ontogenetic development were used. We therefore obtained L. calcarifer and S. serrata from a hatchery, as this was the only way sufficient numbers of these animals at the same stage of ontogenetic development could be obtained. Predator avoidance, however, may be a learned behaviour (Brown and Smith, 1998; Brown and Godin, 1999). In many studies of freshwater larval and juvenile fish, recognition of a specific predator partially arises from associating the chemicals of the predator with chemical alarm cues released from a conspecific that has been caught (reviewed by Smith, 1992; Brown, 2003). Indeed, predation rates on hatchery-reared salmonids are greater than those on wild-born salmonids (Berejikian, 1995). A potential artefact of using hatchery-reared zooplankton in the present study, therefore, was that they had not been previously exposed to C. mosaicus and may not have recognised the jellyfish as a potential predator. The lack of response by S. serrata megalopae to jellyfish water in the flume tank may have reflected their lack of previous exposure to predatory medusae. Greater avoidance of jellyfish water may have also occurred in L. calcarifer larvae if wild caught fish had been used. The potential limitations in using hatchery-reared animals prompted the testing of the readily available, wild-caught juvenile penaeid prawns at Smiths Lake. The prawns co-occurred with the jellyfish at the time of collection and, therefore, had the opportunity to recognise C. mosaicus as a potential predator. Despite this, wild-caught juvenile prawns also failed to respond to the chemicals of the jellyfish.

While the megalopae did not respond to C. mosaicus in the flume tank, the height to which the S. serrata megalopae swam in water column was consistently suppressed when exposed to an oral arm (which provided chemical and visual cues), a sealed oral arm (which provided a visual cue only) or mucus (which provided a chemical cue and a reduced visual cue) of C. mosaicus. The response of the megalopae to these three treatments seems to be based on visual detection of the jellyfish, as this was the only consistent cue across all three treatments. To determine whether the response to visual cues resulted from the specific appearance of the jellyfish, or was simply a response to the shadow cast from an object, similar experiments that incorporate a shadow control could be done. Regardless of the actual mechanism, however, our results suggest that the vertical movement of megalopae may be suppressed when encountering a dense aggregation of jellyfish.

Blooms of jellyfish have the potential to significantly affect the behaviour of at least some zooplankton. Avoidance of jellyfish by zooplankton may increase their rate of survival in the short-term but if blooms of jellyfish are widespread and persistent, the need to repeatedly avoid medusae may ultimately lead to reduced fitness and survival of the zooplankton. For example, growth rates and the ability of zooplankton to feed may be inhibited if large amounts of energy are consistently expended to avoid predation (Nystrom, 2005). Inhibition of vertical migration may also reduce the ability of migratory zooplankton to feed in productive surface waters and reduce the capacity of organisms such as crab megalopae to use selective tidal-stream transport to move to suitable habitats for settlement (Lee et al., 2005). The inability to find suitable settlement habitats often delays development of the meroplankton to subsequent life-history stages (Christy, 1989) and can reduce the fitness of postmetamorphic animals (Gebauer et al., 1999). The indirect effects of the behavioural responses of zooplankton to jellyfish blooms are likely to be difficult to quantify but may be substantial.

368

369 **Conclusions**

370 This study has demonstrated that some species of zooplankton modify their behaviour in the
 371 presence of jellyfish. When evaluating the impacts of jellyfish on pelagic systems, therefore, it is
 372 important to consider not only those species that are caught by, or compete with, the medusae but
 373 also the zooplankton species whose behaviour may be adversely modified during jellyfish blooms.

374

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382

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490 **Table 1** Average ($\pm$ 1 S.E.) absolute abundances of zooplankton present in the water column (number m^{-3}) and on the oral arms of C.
491 mosaicus (number per jellyfish) during the day and night on four occasions between August and November, 2005, in Moreton Bay. P =
492 zooplankton from plankton hauls; O = zooplankton from oral arms; n = number of samples; white rows contain organisms present in the water
493 and on the oral arms; grey rows contain organisms present only in the water column.

	08/08/05				07/10/05				13/11/05				23/11/05			
Functional groups	Day ($\bar{n}$ = 6)		Night ($\bar{n}$ = 6)		Day ($\bar{n}$ = 9)		Night ($\bar{n}$ = 9)		Day ($\bar{n}$ = 9)		Night ($\bar{n}$ = 9)		Day ($\bar{n}$ = 9)		Night ($\bar{n}$ = 6)	
	P	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O
Siphonophores	-	-	-	-	-	-	-	-	3.4 ± 0.9	-	3.4 ± 1.2	-	-	-	-	-
Hydrozoan medusae	2.6 ± 1.7	-	4.3 ± 2.4	-	18.7 ± 6.4	-	4 ± 0.5	-	26.6 ± 6.9	-	50.5 ± 5.1	-	40.2 ± 12.5	-	11.1 ± 3.8	-
Ctenophores	7.7 ± 1.7	-	2.6 ± 1.7	-	2.3 ± 1.2	-	1.7 ± 0.9	-	0.6 ± 0.6	-	2.3 ± 0.9	-	-	-	2.6 ± 1.1	-
Nematodes	-	-	7.7 ± 4.3	-	1.7 ± 1.2	-	2.3 ± 1.2	-	0.6 ± 0.6	-	2.3 ± 2.3	-	-	-	-	-
Chaetognaths <u>Sagitta spp.</u>	5.1 ± 1.9	0.2 ± 0.2	6 ± 2.4	-	51.6 ± 25.8	-	51.6 ± 16	0.1 ± 0.1	11.3 ± 2.9	-	26.6 ± 8.2	-	11.9 ± 4.7	-	75.7 ± 10.2	-
Gastropod veligers	862.3 ± 149.6	3 ± 0.8	527.2 ± 34.3	2.2 ± 0.7	1385.5 ± 134.2	3.3 ± 0.7	666.7 ± 173.9	4.6 ± 7	371.9 ± 59.2	2.7 ± 0.9	402.5 ± 30.8	2.7 ± 0.6	755.1 ± 252.2	5.1 ± 0.7	1551.9 ± 313.3	6.3 ± 1.2
Bivalve veligers	289.1 ± 48.9	12.8 ± 4	935.4 ± 225.6	21.5 ± 4.5	1387.8 ± 255.1	25.9 ± 6.9	594.1 ± 162.9	23.9 ± 10	771 ± 224.9	26.1 ± 4.1	439.9 ± 68.7	33.4 ± 5.7	367.4 ± 114.8	11.3 ± 1.8	780.6 ± 229.5	12.7 ± 4
Cephalopod	-	-	-	-	-	-	-	-	-	-	0.6 ± 0.6	-	-	-	-	-
Polychaete larvae	238.9 ± 17.3	-	205.8 ± 24.8	0.2 ± 0.2	347.5 ± 99.6	0.1 ± 0.1	241.5 ± 28.3	-	156.5 ± 57.6	-	118.5 ± 48.6	-	66.3 ± 11.1	-	131.8 ± 24.9	-
Polychaete adults	9.4 ± 2.8	-	6 ± 3.8	-	42 ± 28.4	-	14.7 ± 10.5	-	1.1 ± 0.7	-	4.5 ± 2.2	-	-	-	1.7 ± 1.1	-
Invertebrate eggs	303.6 ± 88.6	-	53.6 ± 23	-	31.7 ± 12.8	0.2 ± 0.2	43.1 ± 15.3	0.1 ± 0.1	22.1 ± 10.2	-	74.8 ± 23.1	-	32.3 ± 14.4	0.3 ± 0.2	23.8 ± 12.9	0.7 ± 0.4
Copepod nauplii	479.6 ± 34	-	748.3 ± 47.6	-	1236.4 ± 242.5	0.3 ± 0.2	1169.5 ± 127.7	-	773.2 ± 74.5	-	415.5 ± 26	0.3 ± 0.2	1234.7 ± 161.4	0.2 ± 0.1	1932 ± 121.1	0.2 ± 0.2
Calanoids	1429.4 ± 81.4	0.5 ± 0.3	1278.9 ± 36.9	1.3 ± 1	2693.9 ± 229.9	0.3 ± 0.2	2303.9 ± 238	0.1 ± 0.1	2896.8 ± 404	1.8 ± 0.5	1726.2 ± 249.4	3 ± 0.6	1523.8 ± 173.7	0.8 ± 0.1	3485.5 ± 376.9	2.5 ± 1.6
Cyclopoids	776.4 ± 43	1.8 ± 0.4	787.4 ± 35.5	2.5 ± 0.7	2170.1 ± 299.4	0.4 ± 0.2	2422.3 ± 221	1.6 ± 1	1465.4 ± 128.2	0.9 ± 0.3	1452.4 ± 261.6	1.2 ± 0.4	1083.9 ± 204.3	0.2 ± 0.1	1754.3 ± 112.7	0.2 ± 0.2
Harpacticoids	317.2 ± 65.2	0.5 ± 0.3	283.2 ± 27.4	-	729 ± 179.3	0.1 ± 0.1	353.2 ± 63.7	0.1 ± 0.1	278.9 ± 36.3	0.2 ± 0.1	365.1 ± 75.8	0.6 ± 0.3	212.6 ± 75.7	-	341 ± 43.2	-
* <u>Paramacrochiron maximum</u>	-	-	-	-	4.4 ± 4.4	1.4 ± 0.4	0.5 ± 0.5	1.1 ± 0.5	-	1.6 ± 0.5	11.2 ± 4.6	1.6 ± 0.6	8.2 ± 5.6	0.8 ± 0.3	11.7 ± 7.7	0.2 ± 0.2
Isopods	18.7 ± 8	-	9.4 ± 4.6	-	16.4 ± 5.6	-	23.8 ± 9	-	3.4 ± 1.9	-	10.8 ± 5.2	0.1 ± 0.1	26.6 ± 7	0.1 ± 0.1	64.6 ± 24.1	0.2 ± 0.2
Gammarid amphipods	0.2 ± 0.2	6.3 ± 3	1.3 ± 0.6	0.3 ± 0.2	0.4 ± 0.4	-	4.3 ± 1.6	0.1 ± 0.1	0.1 ± 0.1	-	2.8 ± 0.7	0.2 ± 0.1	-	0.2 ± 0.1	2.7 ± 1.9	0.3 ± 0.3
Caprellid amphipods	-	-	0.9 ± 0.9	-	-	-	4.5 ± 1.8	-	-	-	0.6 ± 0.6	-	-	-	0.9 ± 0.9	-
Cladocerans	-	-	-	-	0.6 ± 0.6	-	-	-	-	-	-	-	-	-	-	-

494 **Table 1 Continued**

functional groups	08/08/05				07/10/05				13/11/05				23/11/05			
	Day ($n = 6$)		Night ($n = 6$)		Day ($n = 9$)		Night ($n = 9$)		Day ($n = 6$)		Night ($n = 6$)		Day ($n = 9$)		Night ($n = 9$)	
	P	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O
Ostracods	24.7 ± 7.6	-	26.4 ± 9.7	-	1.1 ± 1.1	-	7.9 ± 5.5	-	2.3 ± 1.2	-	3.4 ± 2.3	-	1.7 ± 1.7	-	5.1 ± 2.6	-
Barnacle nauplii	27.2 ± 9.9	-	55.3 ± 20.2	-	89 ± 36.6	-	62.4 ± 12.4	-	82.8 ± 16.4	-	15.9 ± 6.7	-	82.8 ± 27.5	-	240.6 ± 45.3	-
Barnacle cyprid larvae	6 ± 2.4	-	16.2 ± 3.6	0.7 ± 0.3	14.2 ± 11.7	0.1 ± 0.1	13 ± 5.8	0.2 ± 0.1	-	-	1.1 ± 0.7	-	-	-	-	-
Pycnogonids	-	-	-	-	-	-	0.6 ± 0.6	-	-	-	-	-	-	-	-	-
Cumaceans	-	-	1.7 ± 1.1	-	-	-	9.6 ± 3.6	-	-	-	0.6 ± 0.6	-	-	-	3.4 ± 1.1	-
Shrimp zoea	6.8 ± 2.2	0.2 ± 0.2	0.9 ± 0.9	1.3 ± 1.3	22.7 ± 10.3	-	37.4 ± 14.9	0.1 ± 0.1	5.7 ± 2.6	-	82.2 ± 19.2	0.9 ± 0.2	2.8 ± 1.2	-	62.9 ± 14.8	1.2 ± 0.7
Prawns	-	-	-	-	-	-	1.7 ± 0.9	-	-	-	-	-	-	-	-	-
Brachyuran crab zoea	10.2 ± 2.3	0.2 ± 0.2	3.4 ± 3.4	-	93.5 ± 32.9	0.2 ± 0.1	13.6 ± 8.3	-	59.5 ± 22.8	0.1 ± 0.1	422.9 ± 163.5	10.9 ± 2.9	5.1 ± 3.4	0.1 ± 0.1	34 ± 11	0.3 ± 0.2
Non-brachyuran crab zoea	-	-	-	-	5.7 ± 1.6	-	7.4 ± 2.1	-	109.4 ± 45.8	-	69.7 ± 17.4	-	1.7 ± 0.9	-	32.3 ± 14.1	-
Crab megalopae	-	-	5.1 ± 1.9	-	0.6 ± 0.6	-	2.3 ± 0.9	-	-	-	0.6 ± 0.6	-	-	-	3.4 ± 1.1	-
Lucifer zoea	-	-	-	-	1.7 ± 1.2	-	2.8 ± 1.5	-	6.8 ± 2.7	-	4 ± 1.4	-	5.1 ± 2.4	-	9.4 ± 6.4	-
<u>Lucifer hanseni</u>	0.9 ± 0.9	-	3.4 ± 1.7	-	0.6 ± 0.6	-	17 ± 8.4	-	-	-	9.1 ± 2.2	-	0.6 ± 0.6	-	6.8 ± 1.1	-
Stomatopod larvae	-	-	-	-	-	-	-	-	-	-	1.1 ± 0.7	-	-	-	-	-
Actinotroph larvae of Phoronid	-	-	3.4 ± 2.2	-	-	-	-	-	-	-	-	-	-	-	-	-
Brachiopod Craniacea larvae	18.7 ± 4.7	-	6.8 ± 3.1	-	1.7 ± 1.2	-	1.1 ± 0.7	-	2.3 ± 1.7	-	0.6 ± 0.6	-	-	-	-	-
Echinoderm pluteus larvae	1.7 ± 1.1	-	0.9 ± 0.9	-	0.6 ± 0.6	-	-	-	11.3 ± 2.9	-	-	-	-	-	2.6 ± 1.7	-
Brittle stars	-	-	-	-	-	-	0.6 ± 0.6	-	-	-	-	-	-	-	-	-
Ascidian tadpole larvae	0.9 ± 0.9	-	1.7 ± 1.7	-	-	-	2.8 ± 2.8	-	-	-	-	-	1.1 ± 0.8	-	1.7 ± 1.7	-
Salps	-	-	-	-	-	-	-	-	0.6 ± 0.6	-	-	-	-	-	-	-
Larvaceans	39.1 ± 10.7	-	35.7 ± 5.4	-	229.6 ± 35	-	271 ± 61.8	-	134.9 ± 27.6	-	245.5 ± 38.3	0.8 ± 0.3	100.9 ± 18.5	0.2 ± 0.1	221.9 ± 55.9	2 ± 1.3
Fish larvae	-	-	-	-	4 ± 2.4	-	2.3 ± 1.2	-	3.4 ± 0.9	-	20.4 ± 5.8	0.2 ± 0.1	-	-	7.7 ± 2.6	-

495 * Paramacrochiron maximum is commensal with C. mosaicus (Browne and Kingsford, 2005) and, therefore was not included in analyses.

496 **Table 2.** Results of three-way ANOVA examining variation in the vertical migration of
 497 megalopae of S. serrata among time of day, experiments and treatments. Cochran's C =
 498 0.1498 (NS).

Source	df	MS	<u>F</u>	<u>P</u>	Denominator MS
Time	1	332.14	0.99	0.38	Experiment (Time)
Experiment (Time)	4	334.36	4.22	< 0.01	Residual
Treatment	3	4783.03	27.96	< 0.01	Treatment x Experiment (Time)
Time x Treatment	3	63.79	0.37	0.77	Treatment x Experiment (Time)
Treatment x Experiment (Time)	12	171.08	2.16	0.03	Residual
Residual	48	79.26			

499

Figure Captions

Figure 1 MDS plots of zooplankton assemblages from the water column (white) and oral arms of C. mosaicus (grey) during the day (Δ) and night ($\bigcirc$) on each of four dates sampled in Moreton Bay.

Figure 2 The percentage change in the average number (± 1 S.E.) of S. serrata megalopae, juvenile penaeid prawns and L. calcarifer larvae in the left side of the tank between the Flow Acclimation and Treatment Flow periods among experimental treatments. Positive values indicate movement into the left side of the tank, and negative values indicate movement out of the left side.

Figure 3 Average (± 1 S.E.) height of S. serrata megalopae among treatments for each of the three experiments done during the day (A) and night (B). Alphabetical symbols assigned to error bars indicate significant differences (e.g. a and b) or similarities (e.g. b and b) between heights of megalopae among treatments within each experiment.

Fig. 1

Figure 2
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Fig. 2

Figure 3
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Fig. 3