

Contribution to the Theme Section 'Jellyfish bloom research: advances and challenges'

Mechanisms underlying heterogeneous distribution of moon jellyfish *Aurelia aurita* s.l. across a sharp pycnocline

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ABSTRACT: The vertical distribution pattern of moon jellyfish *Aurelia aurita* s.l. medusae can vary dramatically within the water column, and a sharp pycnocline is one of the major factors that limit vertical distribution. Causes of this limited distribution are likely to be either or both of 2 behavioral responses: a passive response related to buoyancy and/or an active response related to the organism's habitat requirements. However, these causes have yet to be verified. We conducted behavioral and physiological experiments and also performed numerical simulations to elucidate the mechanisms by which a pycnocline may restrict the vertical distribution of jellyfish. Behavioral experiments conducted in 2-layered water tanks showed that (1) salinity discontinuity alone limited the vertical distribution of jellyfish, (2) distribution was restricted to the layer with the same salinity as the jellyfish had physiologically been acclimatized to, and (3) jellyfish did not have any specific salinity or depth preferences. Analyses showed that the jellyfish bodies had a similar density to that of the ambient seawater. When jellyfish were transferred to seawater of a different salinity, they required several hours to acclimatize to the new environment. Our results indicate that jellyfish, when approaching a sharp pycnocline, are subjected to a strong buoyancy force and thus are unable to readily swim across the pycnocline. Numerical simulations also supported the buoyancy hypothesis. Therefore, we conclude that the passive response to the buoyancy force is the primary mechanism underlying the heterogeneous distribution of moon jellyfish across a sharp pycnocline.

KEY WORDS: Vertical distribution · Buoyancy · Swimming behavior · Numerical simulation

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INTRODUCTION

Moon jellyfish *Aurelia aurita* s.l. (see Dawson & Martin 2001, Ki et al. 2008, Chiaverano et al. 2016, Scorrano et al. 2016 for cryptic species for this genus) are euryhaline and highly tolerant to low dissolved oxygen concentrations, attributes which enable them to have a ubiquitous distribution throughout global coastal waters (Miyake et al. 1997, Dawson & Martin 2001, Rutherford & Thuesen 2005, Shoji et al. 2005).

Mass occurrences of this species have been reported from various regions, especially from semi-enclosed embayments (Omori et al. 1995, Uye et al. 2003, Kogovšek et al. 2010, Aoki et al. 2012b, Robinson & Graham 2013), and are recognized to play important roles in ecosystems (Pauly et al. 2009). Moon jellyfish consume zooplankton including fish eggs and larvae and therefore are important predators and competitors of commercial fishes (Bailey & Batty 1983, Möller 1984, Uye & Shimauchi 2005). In addition, some fishes

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feed on jellyfish and utilize them as shelter from predators (Purcell & Arai 2001, Masuda et al. 2008, D'Ambra et al. 2015, Miyajima-Taga et al. 2016). *Aurelia* blooms also have caused negative socio-economic impacts, such as by clogging fishing nets and water intake structures of power plants (Purcell et al. 2007, Dong et al. 2010). Therefore, mechanisms by which these blooms are initiated are of major ecological and major socio-economic interest.

Jellyfish blooms are categorized as true or apparent blooms, which are characterized by either rapid growth of a local population or temporal redistribution of an existing population from an adjacent area (i.e. an invading population), respectively (Graham et al. 2001). Identifying the blooming population as either local or invader is important for understanding the overall population dynamics, because certain cnidarian species do not always show temporally synchronized blooms, even in closely related, geographically adjacent populations (Dawson et al. 2015). For the cnidarian *Rhizostoma octopus*, both genetic analyses and oceanographic dispersal models are effective methods to identify the geographical origin of blooms (Lee et al. 2013). Studies on other planktonic marine organisms show that characteristics of vertical distribution are likely important factors to reconstruct dispersal models (Smith & Stoner 1993, DiBacco et al. 2001, Carr et al. 2008, North et al. 2008, Hubbard & Reidenbach 2015), because the direction and strength of the seawater current can differ between depths. While relatively abundant genetic data on *Aurelia* are available (e.g. Dawson & Jacobs 2001, Dawson & Martin 2001, Ki et al. 2008, Chiaverano et al. 2016, Scorrano et al. 2016), there are few oceanographic dispersion models established that include characteristics of their vertical distribution (Aoki et al. 2012a).

One factor affecting the vertical distribution of *Aurelia* medusae (hereafter referred to as *Aurelia*) is the pycnocline, which frequently restricts *Aurelia* distribution to either the layer above or below it. In the marine lakes of Mljet Island (located in the Adriatic Sea), *Aurelia* are mainly distributed below the thermocline (Malej et al. 2007). Similarly, aggregations in Mikawa Bay, Japan, showed that the shallower boundary of their vertical distribution was restricted by a sharp pycnocline (Suzuki et al. 2016). Similarly, the deeper boundary depth of *Aurelia* aggregations in the Gulf of Mexico was correlated to the pycnocline depth (Churnside et al. 2016). A previous study, which analyzed the vertical distribution of *Aurelia* in multiple Japanese coastal areas, established how the pycnocline restricts the vertical distri-

bution of *Aurelia* (Suzuki et al. 2017). This heterogeneous distribution of *Aurelia* across a sharp pycnocline occurs when the maximum value of the difference in vertical seawater density (σ_t) between adjacent depths in the water column ($\Delta\sigma_{t_{max}}$), which is an index of the stratification strength, is higher than 0.7 to 1.1 kg m⁻³. This phenomenon is caused when lower-salinity waters occupy the surface layers due to freshwater discharge. However, the mechanism by which the pycnocline restricts the distribution of *Aurelia* has yet to be elucidated.

There are 2 possible mechanisms for the pycnocline restriction on *Aurelia* distribution (Graham et al. 2001). The first is *Aurelia*'s preference for specific environmental factors, such as prey abundance, salinity or depth (i.e. the preference hypothesis). A pycnocline acts as a frontal barrier, in which phytoplankton generally show high production, and thus zooplankton abundance is also high (Franks 1992, Schiariti et al. 2006, Luo et al. 2014). In the preference hypothesis, *Aurelia* may actively respond to the pycnocline as a foraging cue. The other possible mechanism is the buoyancy force to which an animal passively responds (i.e. the buoyancy hypothesis). Jellyfish generally adjust their osmolality to the surrounding environment over the duration of several hours (Mills 1984, Nielsen et al. 1997, Wright & Purcell 1997). In the buoyancy hypothesis, *Aurelia* attempting to cross the pycnocline are effectively pushed back into the original layer that their osmolality is equilibrated to due to the overall difference in relative buoyancy between the 2 layers. That is, due to the difference in density between the body of *Aurelia* and the seawater in the new layer, the relatively more or less dense body of the jellyfish compared to the new layer prevents them from moving into the upper or lower layers of the pycnocline, respectively. Given the jellyfish's relatively low swimming ability relative to its large body size, it would be difficult for the jellyfish to overcome the buoyancy force in this scenario. Since multiple environmental factors generally show large variations across the pycnocline *in situ*, it is often difficult to estimate independent effects from field observations. Thus, neither of these hypotheses has been verified yet.

In the present study, the objective was to elucidate the mechanisms that restrict the vertical distribution of jellyfish relative to the pycnocline. We first conducted experiments on the relationship between densities of the *Aurelia* body and the ambient seawater. We then performed behavioral experiments in 2-layered (stratified) tanks, which simulated a pycn-

ocline. To estimate the likelihood of the buoyancy hypothesis, we also conducted numerical simulations. In addition, we numerically assessed if the jellyfish's low swimming ability in relation to its body size, which is a distinctive feature among marine organisms (Acuña et al. 2011), plays an important role in the pycnocline-restricted vertical distribution.

MATERIALS AND METHODS

Expt 1: *Aurelia* body density

We compared the body density of *Aurelia aurita* s.l. to that of ambient seawater. *Aurelia* (bell diameter: 13.8 ± 1.1 cm, mean \pm SD) were collected from Maizuru Bay, Japan (35.49° N, 135.37° E), and transferred to tanks (40 cm length \times 26 cm width \times 30 cm height, 26 l) with a temperature of 25° C and salinities of 21, 25, 29, 33 or 37. Temperature and salinity were measured with a YSI 600QS multiparameter water quality sonde, and seawater density was calculated from the temperature and salinity data (UNESCO 1983). After 12 h of acclimatization, the body densities of 3 individual *Aurelia* were calculated from each salinity tank. Body density (ρ_{jelly}) was estimated from the difference in the measured body weights of *Aurelia* while submerged in water (W_{jelly1} and W_{jelly2}) across 2 tanks (tank 1 and tank 2) with different seawater densities (ρ_{SW1} and ρ_{SW2} , respectively). To measure *Aurelia* body weights, we attached each specimen with a fine thread from a rod horizontally attached to an electronic scale (EK-2000i, A&D), which was placed on a plastic board set over the tanks (Fig. 1). W_{jelly1} and W_{jelly2} are expressed as follows:

$$W_{\text{jelly1}} = \text{Vol}_{\text{jelly}}(\rho_{\text{jelly}} - \rho_{\text{SW1}}) \quad (1)$$

$$W_{\text{jelly2}} = \text{Vol}_{\text{jelly}}(\rho_{\text{jelly}} - \rho_{\text{SW2}}) \quad (2)$$

where $\text{Vol}_{\text{jelly}}$ is the volume of the *Aurelia*'s body, and ρ_{SW1} and ρ_{SW2} are the densities of seawater in tank 1 and tank 2, respectively. In Eqs. (1) & (2), ρ_{jelly} is expressed in the following equation:

$$\rho_{\text{jelly}} = \frac{W_{\text{jelly1}} \times \rho_{\text{SW2}} - W_{\text{jelly2}} \times \rho_{\text{SW1}}}{W_{\text{jelly1}} - W_{\text{jelly2}}} \quad (3)$$

We also estimated the turnover rate of *Aurelia* body density, which is the rate of change in body density during acclimatization to a different seawater density. *Aurelia* were transferred from a 25° C tank with salinity 33 to another 25° C tank with salinity 25. Before the transfer, *Aurelia* were acclimatized to the

tank with salinity 33 for 12 h. Body densities of the 3 *Aurelia* were measured 0, 0.5, 1, 2, 2.5, 3, 4, 5, 6, 8, 10 and 12 h after the transfer. To estimate the turnover rate, we expressed ρ_{jelly} at time t as follows:

$$\rho_{\text{jelly}} = \rho_{\text{SW}}^1 + (\rho_{\text{SW}}^0 - \rho_{\text{SW}}^1)e^{-\frac{t}{\gamma}} \quad (4)$$

where ρ_{SW}^0 and ρ_{SW}^1 are the density of seawater in which *Aurelia* was originally acclimatized and to which *Aurelia* was transferred, respectively; γ is a parameter related to the physiological rate of response of ρ_{jelly} change and was estimated with the nls function of R 3.3.0. Eq. (4) assumes that ρ_{jelly} is the same as the *Aurelia*'s body density in ambient seawater after acclimatization and that the turnover rate is proportional to the density difference between the body of *Aurelia* and the ambient seawater.

Expt 2: *Aurelia* behavior in relation to an artificially formed pycnocline

We conducted behavioral experiments to observe the response of *Aurelia* to a pycnocline. *Aurelia* (bell diameter: 12.8 ± 0.5 cm) were collected from Tokyo Bay, Japan (35.61° N, 139.98° E), and acclimatized in one of two 25° C tanks (salinity 25 or 33) for 12 h. According to the results of Expt 1, this duration is long enough for *Aurelia* to acclimatize their body density to the ambient seawater. The acclimatized *Aurelia* were then transferred to control tanks and experimental (2-layered) tanks. All

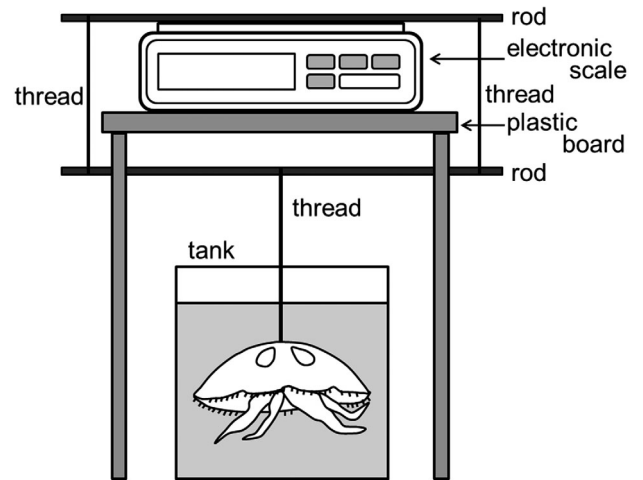


Fig. 1. Setup for weighing *Aurelia* in a tank. *Aurelia* were attached by a fine thread from a rod horizontally attached to an electric scale, which was placed on a plastic board set over the tanks

tanks were 50 cm length × 50 cm width × 65 cm height (125 l). The two 25°C control tanks were filled with seawater of either salinity 25 or 33, which maintained the conditions of the 2 acclimatization tanks. Seawater in the 2 experimental tanks consisted of a layer of salinity 25 seawater over a layer of salinity 33 seawater. *Aurelia* acclimatized to salinity 25 were transferred to the salinity 25 control tank and a 2-layered experimental tank, while *Aurelia* acclimatized to salinity 33 were transferred to the salinity 33 control tank and a 2-layered experimental tank (see Fig. 4). The swimming behaviors of 4 *Aurelia* individuals transferred together to each tank were video recorded (iVIS HFM52, Canon), and their positions in the tanks were observed every minute for 30 min. All observations were made under constant vertical lighting in a constant temperature room at 25°C. These behavioral experimental trials were replicated twice for each tank setting. The water in the 2-layered experimental tanks remained stratified throughout the 30 min experiments, and the thickness of the pycnocline (i.e. the density gradient between the layers of different salinity) was about 10 cm. No prey or water flow was provided to the tanks during trials to eliminate potential effects on *Aurelia* behavior. Temperature and salinity were measured with a YSI 600QS multiparameter water quality sonde.

Numerical simulations

The buoyancy hypothesis relies only on kinetic mechanics. Therefore, if the buoyancy hypothesis is the major mechanism of the heterogeneous distribution of *Aurelia* across a sharp pycnocline, the *in situ* response of *Aurelia* to a pycnocline would be numerically replicable based on kinetic mechanics. To validate the buoyancy hypothesis, we compared the threshold value of the vertical seawater density difference to restrict *Aurelia* distribution estimated from the following numerical simulation to that obtained from *in situ* observations ($\Delta\sigma_{t\max} = 0.7$ to 1.1 kg m⁻³, Suzuki et al. 2017). In the numerical simulation, we assumed a case where an *Aurelia* that was fully acclimatized to the bottom layer (density: $\rho_{SW\alpha}$) in a 2-layered stratified tank swims toward the surface layer (density: $\rho_{SW\beta}$). The body density of the *Aurelia* (ρ_{jelly}) was assumed to be constant and at the same density as the seawater in the bottom layer ($\rho_{SW\alpha}$). Temperature and salinity of the bottom layer were set at 20°C and salinity 33, respectively. The numerical analysis was performed for *Aurelia* with

bell diameters of 10 to 25 cm, which is a usual size range in aggregations in Japanese coastal areas (Yasuda 1975, Ishii & Tanaka 2006, Shoji et al. 2010, Aoki et al. 2012b).

In the numerical simulation, we calculated hydrodynamic forces of *Aurelia* in the surface layer to estimate swimming speed of *Aurelia* in the surface layer. Based on Daniel (1983) and McHenry & Jed (2003), we modeled the hydrodynamics of jellyfish swimming as the sum of thrust (T), drag (D), the acceleration reaction force (A), the force required to accelerate the mass of the jellyfish itself (F) and gravity force (G). This model is expressed in an equation of motion as follows:

$$F = T + D + A + G \quad (5)$$

T (T_{jet} in McHenry & Jed 2003), D , A and F , were calculated as in McHenry & Jed (2003). Bell diameter and body height of *Aurelia*, which affect T , D , A and F , were considered fluctuating during their pulsation. Time-dependent bell diameter $d(t)$ and height $h(t)$ at time t were modeled as trigonometric functions as follows:

$$d(t) = 0.5 d_{\text{range}}(\cos(\pi k(t)) - 1) + d_{\text{rest}} \quad (6)$$

$$h(t) = 0.5 h_{\text{range}}(\cos(\pi k(t)) - 1) + h_{\text{rest}} \quad (7)$$

where d_{rest} and h_{rest} are the resting bell diameter and height, respectively, and d_{range} and h_{range} are the ranges of the values in bell diameter and height, respectively. All of the 4 variables, d_{rest} , h_{rest} , d_{range} and h_{range} , were estimated from size-dependent equations in McHenry & Jed (2003). $k(t)$ is a sawtooth function, which changes linearly over time t , from values of 0 to 1 over the duration of the contraction phase, and then decreases to 0 over the recovery phase (McHenry & Jed 2003). Pulse frequency (f [Hz]) and proportion of the pulsation cycle spent in contraction (q) were given as 0.55 Hz and 0.42, respectively, based on *in situ* results from the following SCUBA diving observations. SCUBA diving observations were conducted to record pulsation behavior of *Aurelia* individuals with a video camera (iVIS HF20, Canon) in Mikawa Bay (34.70° N, 137.10° E), Japan, from May to September 2013. Ten pulsation cycles for each individual were analyzed to obtain f and q ($n = 5$, bell diameter: 15 to 21 cm, mean $f = 0.50 \pm 0.11$, mean $q = 0.44 \pm 0.02$). G was calculated as follows:

$$G = (\rho_{SW\beta} - \rho_{\text{jelly}})\text{Vol}_{\text{jelly}} g \quad (8)$$

where g is the gravity acceleration (9.81 m s⁻²). $\text{Vol}_{\text{jelly}}$ was estimated from relationships between the bell diameter to wet weight (m) ratio (McHenry & Jed

2003) and wet weight to body volume ratio ($m[\text{kg}] = 1.021 \text{ Vol}_{\text{jelly}} [l]$, Ohshima et al. 1967). As we assumed ρ_{jelly} was the same as $\rho_{\text{SW}\alpha}$, Eq. (8) can be expressed as follows:

$$G = -\Delta\rho_{\text{SW}\alpha-\beta} \text{Vol}_{\text{jelly}} g \quad (9)$$

where $\Delta\rho_{\text{SW}\alpha-\beta}$ is the difference in seawater densities between the 2 layers. F acted against the force to change the inertia of the body, which was expressed in the following equation (McHenry & Jed 2003):

$$F = m(\Delta U/\Delta t) \quad (10)$$

where U is the swimming speed of *Aurelia* and was calculated in the simulations from 5 pulsation cycles that followed an initial 3 cycles upon the start of swimming according to McHenry & Jed (2003).

The accuracy of the present simulation was evaluated by comparison of the mean swimming speed predicted from the simulation with speeds measured by the following stereo camera procedure (observed swimming speed), which was similar to that described in Matanoski et al. (2004). Seven *Aurelia* (bell diameter: 11 to 17 cm) collected from Tokyo Bay (35.55° N, 139.98° E) were individually stored in a transparent tank. The tank was a 50 cm cube filled with seawater (25°C and salinity of 25). Approximately 0.05 ml of an elastomer fluorescent tag (Northwest Marine Technology) was injected into the top of the *Aurelia* bell and illuminated by UV fluorescent lights (Aceline lamp, Nippo Electric), which were installed over the tank. The fluorescent tag and the UV lights did not show significant effects on the pulsation of *Aurelia*, f and q (2-way repeated measures ANOVA with paired comparison; $n = 6$; bell diameter: 9 to 10 cm; f , tag: $p = 0.09$, UV: $p = 0.17$, tag \times UV: $p = 0.46$; q , tag: $p = 0.09$, UV: $p = 0.55$, tag \times UV: $p = 0.92$). The 3-dimensional behaviors of *Aurelia* were measured by tracking the fluorescent tag with a stereo camera system. Two cameras (C920r, Logi-cool) were placed in front of the transparent tank and connected to a personal computer which controlled synchronization of the cameras. The cameras recorded the fluorescent images twice a second for an hour. The 3-dimensional real-space coordinates of the fluorescent tag were transformed from the image coordinates by third-order polynomials, which are effective to prevent erroneous localization due to wall effects on the reflective indices between water and air at the tank walls and to reduce calibration errors (Watanabe et al. 2006). To avoid wall effects on *Aurelia* swimming, only those swimming tracks that were more than 5 cm from the walls were utilized to calculate the mean swimming speed.

The threshold value of the vertical seawater density difference to restrict *Aurelia* distribution in the numerical simulations was defined as the value observed when the mean swimming speed of *Aurelia* in the new layer equaled 0. We estimated the threshold values for *Aurelia* with bell diameters ranging from 10 to 25 cm with 1 cm intervals, and then those values were averaged. Swimming speeds of *Aurelia* under $\Delta\rho_{\text{SW}\alpha-\beta}$ of 0.7 to 1.1 kg m^{-3} , which is the *in situ* observed threshold value to restrict their vertical distribution (Suzuki et al. 2017), were also estimated and then compared to that at $\Delta\rho_{\text{SW}\alpha-\beta}$ of 0 kg m^{-3} .

The low swimming speed of jellyfish compared to their large body makes them distinguishable from fish and other marine organisms (Acuña et al. 2011). In the present study, we evaluated an effect of this characteristic of jellyfish on their swimming ability to cross a pycnocline with a sensitivity analysis for their body size. The sensitivity analysis consisted of considering different ratios of body size to swimming ability based on varying body size (from half to twice the actual size, which was 20 cm in diameter in the simulation)—which affected drag D and acceleration reaction force A —and constant thrust T , which was the same as the actual thrust.

RESULTS

Expt 1: *Aurelia* body density

After the 12 h acclimatization phase, the body density of *Aurelia aurita* s.l. closely approximated that of the ambient seawater, with a difference (mean \pm SD) of only $0.05 \pm 0.28\%$ (Fig. 2). In the turnover rate experiment, *Aurelia* body density became closer to that of the new environment over time (Fig. 3). The equation to calculate the density change in *Aurelia* body composition over time was estimated as follows:

$$\rho_{\text{jelly}} = \rho_{\text{SW}}^1 + (\rho_{\text{SW}}^0 - \rho_{\text{SW}}^1) e^{\frac{-t}{0.08535}} \quad (11)$$

According to the equation, *Aurelia* was estimated to require ~ 4 h to become 99% acclimatized to the new environment (i.e. *Aurelia* body density was only $\sim 1\%$ different from the density of ambient seawater).

Expt 2: *Aurelia* behavior in relation to an artificial pycnocline

In the behavioral experiments, there was a clear difference in *Aurelia*'s vertical positions (i.e. depth)

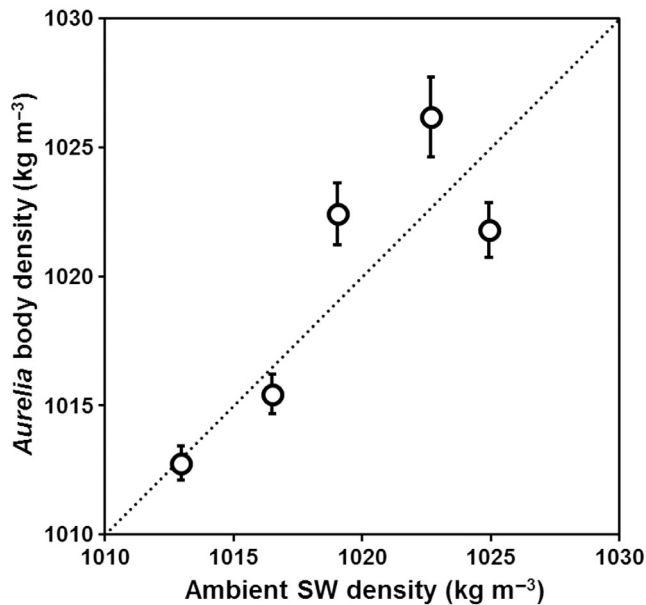


Fig. 2. Relationship between densities of *Aurelia* (mean \pm SD, $n = 3$) and the ambient seawater (SW). The dashed line indicates a 1:1 relationship

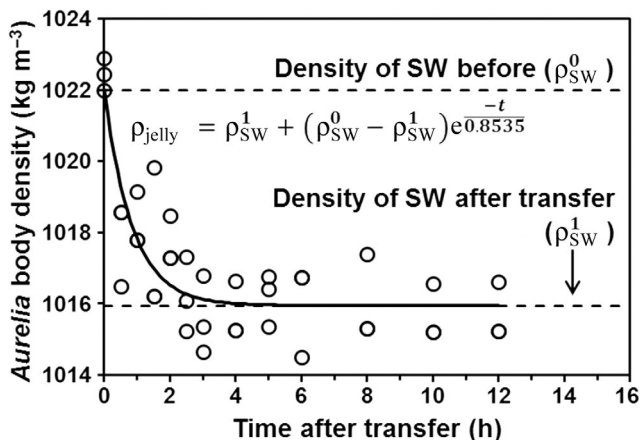


Fig. 3. Change in *Aurelia* body density over time. The open circles and solid line indicate the observed and model-predicted body densities of *Aurelia*, respectively. SW: seawater

between the control and the 2-layered experimental tanks (Fig. 4). In the 2 control tanks with single-salinity seawater, *Aurelia* utilized all depths, from the bottom to the surface (case 1 and case 4 in Fig. 4). In contrast, in the 2-layered tanks, distribution of *Aurelia* was restricted by the pycnocline: *Aurelia* from both of the 2 different acclimatization tanks mainly stayed in the layer with the same seawater density that they were originally acclimatized to and did not move to the other layer until the end of the experimental trials (case 2 and case 3 in Fig. 4). *Aurelia* in the 2-layered tanks did not show any specific prefer-

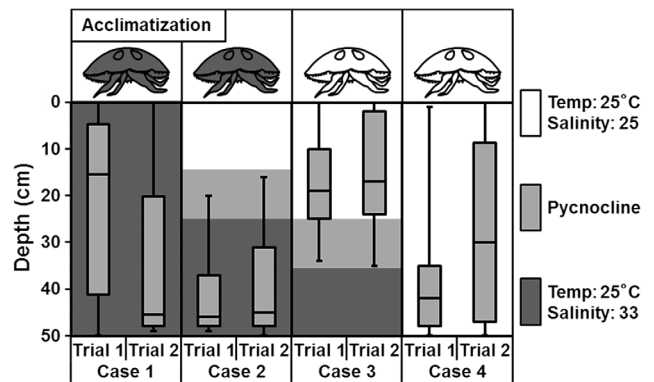


Fig. 4. Vertical position of *Aurelia* in mixed (control) and 2-layered (experimental) tanks. Horizontal lines inside each box indicate median depth values for the 4 *Aurelia* individuals during each 30 min experiment (1 min interval observations, $n = 124$). Boxes: 25th and 75th percentiles, whiskers: range. Background colors show water column structures. Colors of *Aurelia* on the top indicate types of seawater in which the *Aurelia* individuals were acclimatized. Temp: temperature

ences for a salinity (e.g. higher salinity) or depth (e.g. deeper layer).

Numerical simulations

In the numerical simulations, predicted swimming speed for *Aurelia* with a bell diameter of 11 to 17 cm in a non-stratified water column ($1.7 \pm 0.3 \text{ cm s}^{-1}$) was slightly lower than, but still comparable to, speeds observed with the stereo camera system ($2.2 \pm 0.4 \text{ cm s}^{-1}$, Fig. 5). From the numerical simulation, the threshold value of the strength of stratification ($\Delta\rho_{\text{SW}\alpha-\beta}$) that restricts *Aurelia* distribution was estimated to be $1.6 \pm 0.4 \text{ kg m}^{-3}$ and was higher than that estimated from the *in situ* observations of *Aurelia* vertical distribution (0.7 to 1.1 kg m^{-3} , Suzuki et al. 2017). The numerical simulation also showed that swimming speeds in the upper layer under $\Delta\rho_{\text{SW}\alpha-\beta}$ of 0.7 and 1.1 kg m^{-3} were ~ 55 and $\sim 40\%$, respectively, of the estimated speeds under an unstratified condition, where $\Delta\rho_{\text{SW}\alpha-\beta}$ was 0 (Fig. 5). From the sensitivity analysis considering different ratios of body size to swimming ability, it was estimated that a hypothetical jellyfish, which had a smaller body size and the same thrust as an actual jellyfish, would be able to swim across a sharper pycnocline than the actual jellyfish would, e.g. $\Delta\rho_{\text{SW}\alpha-\beta}$ for a half-sized jellyfish was approximately 9 times higher than that for a full-sized jellyfish when the mean swimming speed was 0 cm s^{-1} (Fig. 6).

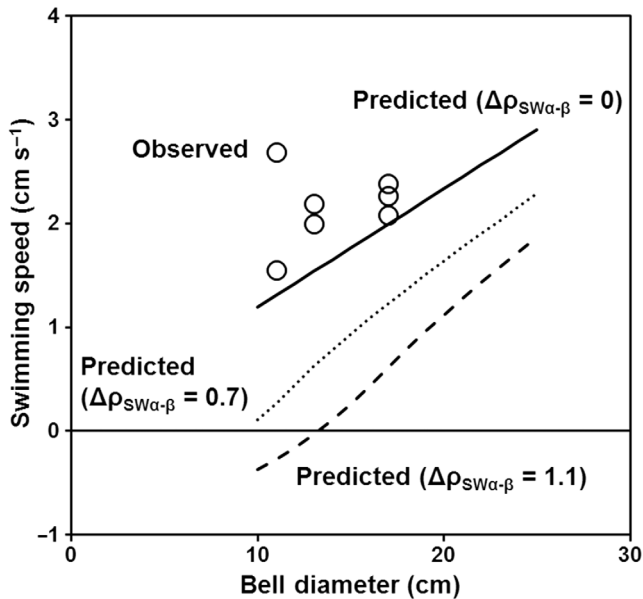


Fig. 5. Swimming speed of *Aurelia*. Open circles and solid line indicate swimming speed in a non-stratified water column observed with a stereo camera system and predicted from a numerical simulation, respectively. The dashed lines are the predicted swimming speeds of *Aurelia* required for crossing a sharp pycnocline in seawater with density differences ($\Delta\rho_{sw\alpha-\beta}$) of 0.7 and 1.1 kg m^{-3} . These density differences are in the 90% range of observed *in situ* threshold values that restrict *Aurelia* distribution (Suzuki et al. 2017)

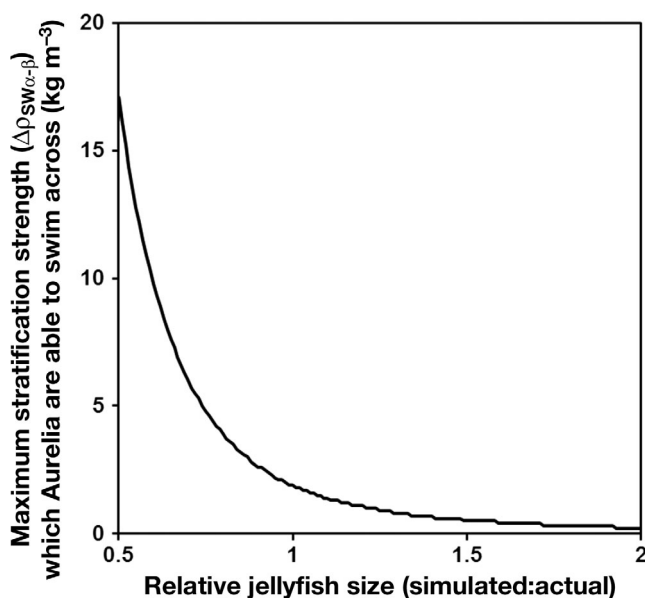


Fig. 6. Maximum stratification strength that *Aurelia* are able to swim across versus *Aurelia* relative body size. In the simulation, the size of *Aurelia* varied from one-half to twice the actual size (1 on the x-axis indicates the actual size), while thrust was constant and the same as what was estimated for the actual-size jellyfish. *Aurelia* were assumed to be able to swim across a pycnocline as long as their mean swimming speed was greater than 0 cm s^{-1}

DISCUSSION

Aurelia body density

Many gelatinous zooplankters have the same or a similar body density to that of the ambient seawater (neutrally buoyant), which helps them to maintain their position in the water column (Mills 1984, Wright & Purcell 1997, Tsukamoto et al. 2009). In the present study, body density of *Aurelia aurita* s.l. also showed values similar to the density of the ambient seawater (Fig. 2). This is consistent with a report that *Aurelia* osmotically become more dense as salinity increases (Hirst & Lucas 1998). More than 95% of the *Aurelia* body volume consists of water (Lucas 1994, Wright & Purcell 1997). When jellyfish are exposed to a higher salinity, their weight increases to maintain buoyancy by selectively exchanging ions (Macallum 1903, Robertson 1949, Wright & Purcell 1997). The time required for jellyfish to adjust their osmolality to different-salinity water varies among species. When salinity decreases by 25% (which is the same degree of change in salinity as in Expt 1 of the present study [from 33 to 25]), hydromedusae and ctenophores require 1 to 20 h to acclimatize to the new salinity (Mills 1984). The results of the present study fall within this range (4 h for 99% acclimatization, Fig. 3). This ability of jellyfish to adapt their osmolality to be neutrally buoyant differentiates them from crustacean zooplankton or fish.

Mechanisms of heterogeneous distribution of *Aurelia* across a sharp pycnocline

Behavioral experiments in the present study suggest that the observed *in situ* heterogeneous distribution of *Aurelia* across a sharp pycnocline can best be explained by the buoyancy hypothesis. In Expt 2, the distribution of *Aurelia* in the 2-layered tanks was restricted by the simulated pycnocline (Fig. 4), similar to observations made *in situ* (Malej et al. 2007, Churnside et al. 2016, Suzuki et al. 2016, 2017). Based on the results from Expt 1, body density of the *Aurelia* specimens in the 2-layered tanks of Expt 2 was expected to be similar to the water density in the tank in which they had been acclimatized. Therefore, *Aurelia* in Expt 2 that were attempting to cross over the simulated pycnocline were pushed back to the original layer, which provided the same seawater density as that in the tank in which they had been acclimatized. *Aurelia* require approximately 4 h to adjust their osmolality to a new environment differing from the

original environment by a salinity of 8 (Fig. 3). This indicates that *Aurelia* would not be neutrally buoyant in the new layer because they would be immediately pushed back to the original layer before becoming acclimatized. *Aurelia* are weak swimmers (swimming speed: 1 to 3 cm s⁻¹) (our Fig. 5; Bailey & Batty 1983, McHenry & Jed 2003); thus, to overcome the physical barrier caused by the differences in relative seawater density between 2 water layers, they would need to exert a strong push/thrust force when faced with a sharp pycnocline. Therefore, our experimental results support the buoyancy hypothesis.

The threshold value of the vertical seawater density difference that would restrict *Aurelia* vertical distribution differed between the numerical simulation (1.6 kg m⁻³) and the *in situ* observation (0.7 to 1.1 kg m⁻³, Suzuki et al. 2017). To cross a pycnocline and remain in the new layer, *Aurelia* would need to maintain swimming for a relatively long period before becoming acclimatized (Fig. 3). In the simulation, we assumed that *Aurelia* continually maintained maximum swimming speed when faced with the stressor, i.e. the buoyancy force effectively pushing *Aurelia* back into the original layer. However, sustainable swimming speeds of marine organisms are usually much lower than their maximum speeds. For 9 species of reef fish larvae that are relatively poor swimmers (as jellyfish are), sustainable swimming speeds were estimated as approximately half of the maximum swimming speed (Fisher & Wilson 2004). Similarly, for larvae of 3 temperate fish species, maximum swimming speeds estimated in laboratory experiments were 2 to 2.5 times greater than *in situ* sustainable swimming speeds (Leis et al. 2006). In the numerical simulation, swimming speeds of *Aurelia* experiencing the *in situ* threshold value of the seawater density difference were estimated to be at about 40 to 55% of maximum speeds, which were observed under a $\Delta\rho_{\text{SW}\alpha-\beta}$ of 0 (Fig. 5). These rates of decrease were similar to those of the fish larvae (Fisher & Wilson 2004, Leis et al. 2006). Assuming that the ratio of sustainable swimming speed to maximum swimming speed for *Aurelia* is similar to that observed in larval fish, using a sustainable swimming speed to estimate the threshold value of the seawater density difference (1.1 kg m⁻³) is suggested, as this may more accurately reflect observations documented *in situ* (0.7 to 1.1 kg m⁻³, Suzuki et al. 2017). Thus, the numerical simulation also supports the buoyancy hypothesis.

Experimental results did not support the preference hypothesis. In Expt 2, the distribution of *Aurelia* in the 2-layered tanks was restricted by the simu-

lated pycnocline even without the provision of prey organisms to *Aurelia* (Fig. 4). Additionally, *Aurelia* did not show preference for a specific salinity. This suggests that the preferences of *Aurelia* for prey organisms or salinity are not essential cues for restricting *Aurelia* distribution under a strongly stratified pycnocline. Based on the buoyancy hypothesis, *Aurelia*'s low swimming speed renders it incapable of crossing a sharp pycnocline with $\Delta\sigma_{\text{t max}}$ higher than the *in situ* threshold value of 0.7 to 1.1 kg m⁻³, even if the environment beyond the pycnocline is more favorable. In Japanese coastal areas, it has been reported that the *in situ* threshold value of $\Delta\sigma_{\text{t max}}$ (0.7 to 1.1 kg m⁻³) was observed only when sea surface salinity decreased from 33 to 29 or less because of high freshwater discharge; however, coastal areas are often less stratified than the *in situ* threshold value of $\Delta\sigma_{\text{t max}}$ (Suzuki et al. 2017). Under these less stratified conditions, *Aurelia* may be able to swim across the pycnocline, and the abundance of prey organisms, such as copepods (Ishii & Tanaka 2001), or specific salinities may affect vertical distributional patterns of *Aurelia*.

A. aurita has been recognized as a nearly ubiquitous species (Dawson & Jacobs 2001), and genetic studies also identified cryptic variants (Dawson & Martin 2001, Dawson et al. 2005). Specimens from Japan and those from Australia and California, USA, make up a single genotype and have been temporarily designated as *Aurelia* sp. 1, which we focused on in the present study (Dawson & Jacobs 2001, Dawson et al. 2005, Ki et al. 2008). *Aurelia* sp. 1 was recently given the full scientific name of *Aurelia coerulea* (Scorrano et al. 2016). *A. coerulea* was reported to have a different physiological response (i.e. asexual reproduction rate) to temperature and prey abundance cues during the benthic polyp stage compared to those of *A. relictata*, which used to be classified as one of the cryptic variants of *A. aurita* (Hubot et al. 2017). Therefore, swimming ability and body density may also be different among *Aurelia* spp., and thus threshold values of $\Delta\sigma_{\text{t max}}$ to restrict their vertical distribution and the mechanisms behind the restricted distributions are potentially species specific.

Jellyfish are characterized by a watery body with low body density and a relatively low swimming speed, which results in a low prey searching efficiency, as opposed to fish, which show the opposite traits. Acuña et al. (2011) suggested that jellyfish have evolved their large watery body, which increases prey contact rates, to achieve a production rate comparable to fish despite low prey searching efficiency. In coastal areas where *Aurelia* blooms fre-

quently occur, phytoplankton and zooplankton, which are prey of *Aurelia*, are often more abundant in the surface layer (Magnesen et al. 1989, Itoh et al. 2011, Watanabe et al. 2017). The surface layer is characterized by low salinity and high nutrients, as it is more affected by river discharge than deeper, more saline waters (Watanabe et al. 2017). When in the deeper, more saline waters, *Aurelia* do not have access to the abundant prey found in the surface layer, as they lack the swimming ability to pass through the pycnocline. It seems paradoxical that the large body that should allow them to capture more prey (Acuña et al. 2011) can prevent them from distributing to the lower-salinity layer containing more prey (Fig. 6), even though they are highly tolerant to low salinity (Miyake et al. 1997). Remaining in a preferred area/habitat is important for maintaining a healthy population, particularly for exploiting good foraging conditions that promote rapid growth. River-sourced, low-salinity waters drive density currents. In semi-enclosed embayments, where mass occurrences of *Aurelia* have been frequently reported (Omori et al. 1995, Uye et al. 2003, Aoki et al. 2012b, Robinson & Graham 2013), particles in the low-salinity surface layer tend to be flushed offshore. The scyphomedusa *Rhizostoma octopus* horizontally swims against the current so that it is not dispersed offshore and thus has been able to maintain its population in the Mediterranean Sea (Fossette et al. 2015). However, the dominant swimming directions of *Aurelia* in their aggregations are generally upward or downward, and they rarely swim horizontally except in shear flows (Costello et al. 1998, Rakow & Graham 2006), although they can swim horizontally to form aggregations in Saanich Inlet, which is a fjord located in British Columbia, Canada (Hamner et al. 1994). Therefore, if *Aurelia* move into the low-salinity surface layer, they are likely to be dispersed offshore and are not able to maintain the population in the area. *Aurelia* generally require a planktonic period of several months to become mature after being released as an ephyra (Lucas 2001). The inability of *Aurelia* to swim across a sharp pycnocline may be an important factor for maintaining their planktonic population in a bloom-forming area for long periods. Therefore, their relatively large and watery body has potentially evolved not only because it is advantageous for prey capture but also because it allows *Aurelia* to remain in a preferred coastal area.

The results of the present study, which focused on both laboratory experiments and numerical simulations, suggest that the predominant factor restricting the distribution of *Aurelia* across a sharp pycnocline

is their passive response to buoyancy generated from a difference in density between their body and the seawater. On the other hand, preferences of *Aurelia* for prey abundance or specific salinities do not appear to be essential cues for the restricted distribution. Quantitative parameters regarding *Aurelia* body density relative to the density of ambient seawater were also provided. These findings can be directly applied to transportation models analyzing *Aurelia* population dynamics and are also important for understanding possible reasons why jellyfish have evolved gelatinous bodies.

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