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Can *Aurelia* (Cnidaria, Scyphozoa) species be differentiated by comparing their scyphistomae and ephyrae?

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Abstract. Debate exists regarding the number of species of the moon jellyfish (genus *Aurelia*), a common member of the planktonic community of the coastal shelf seas around the world. Three *Aurelia* congeners (*A. aurita*, *A. labiata* and *A. limbata*) are currently considered to exist but recent genetic analyses suggested that this is an oversimplification. We analyzed the morphological characteristics of scyphistomae, morphological characteristics of ephyrae and differences in the time span of the strobilation process of *Aurelia* congeners from 17, 7 and 6 different source populations, respectively, of known species. Morphological characteristics of scyphistomae were similar among the 17 populations but those of ephyrae, such as the shape and form of lappets, were effective discriminators in the 6 cases examined. We recommend identifying species based on differences in 1) the morphological characteristics of scyphistomae and ephyrae (and not only medusae), 2) the genetics of individuals, and 3) the geographical occurrence of the population. This study adds to the growing body of knowledge on scyphozoan scyphistomae and ephyrae, stages of the metagenic life cycle of scyphozoans that have received relatively little study compared to medusae.

Keywords. Polyps, jellyfish, strobilation, nomenclature, morphology.

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Introduction

The perceived increased frequency of blooms of jellyfish in the world's ocean (Mills 2001; Purcell *et al.* 2007; Purcell 2012; Condon *et al.* 2012, 2013; Lee *et al.* 2013) has intensified research efforts to understand the population dynamics of gelatinous plankton, with the majority of research having been conducted on the conspiculous medusoid life stages (Lucas *et al.* 2012). Medusae in the genus *Aurelia* Lamarck, 1816 have been reported to occur in the world's oceans from 70° N to 40° S where they are most commonly found along continental shelves or close to large islands (Mayer 1910; Kramp 1961; Russell 1970; Miyake *et al.* 2002; Schroth *et al.* 2002). Despite >100 years of research on *Aurelia*, the

taxonomy of the genus is still unclear. The genus was originally described as '*Aurellia*', which was changed to '*Aurelia*' by Rees (1957). It had three species: *A. aurita* (Linné, 1758), the Pacific *A. labiata* Chamisso & Eysenhardt, 1820 and *A. maldivensis* Bigelow, 1904 from the Indian Ocean (Linné 1758; Chamisso & Eysenhardt 1820; Bigelow 1904). Debate existed on whether *A. labiata* and/or *A. limbata* Brandt, 1838 were valid members of the genus (Brandt 1838). Kramp (1961) described six different species of *Aurelia*, whereas Russell (1970) declared that only *A. aurita* and *A. limbata* were valid species. Gershwin (2001) provided a new description of *A. labiata* and reported it to be endemic to coastal areas of the Eastern Pacific. Although three species (*A. aurita*, *A. labiata* and *A. limbata*) are currently morphologically considered to comprise the genus (Wrobel & Mills 1998; Gershwin 2001; Miyake *et al.* 2002; Albert 2005; Widmer 2005), genetic analyses have suggested a more complex situation, including five cryptic species of *Aurelia* in the North Pacific and up to nine species worldwide (Dawson & Jacobs 2001; Dawson & Martin 2001; Schroth *et al.* 2002; Dawson 2003; Dawson *et al.* 2005).

The vast majority of studies using morphology to distinguish species of *Aurelia* has examined medusae, while only five studies (Uchida & Nagao 1963; Gershwin 2001; Straehler-Pohl 2009; Straehler-Pohl & Jarms 2010; Straehler-Pohl *et al.* 2011) have considered the morphology of scyphistomae and ephyrae. It is known that scyphistoma populations of scyphozoan jellyfish can be distinguished not only by using morphological features but also by analyzing asexual propagation as well as the timing and intermittency of strobilation (e.g., Condon 2001; Lucas 2001; Ma & Purcell 2005; Willcox *et al.* 2007; Adler & Jarms 2009; Straehler-Pohl 2009; Holst 2012a). Documenting the morphological characteristics of scyphistomae and ephyrae can not only (potentially) help clarify the taxonomic status of the genus *Aurelia*, but advancing our knowledge on the strobilation of *Aurelia* scyphistomae is also an important step towards understanding the bloom dynamics of members of this genus (Lucas 2001; Purcell 2007; Purcell *et al.* 2012).

We examined aspects of the morphology of scyphistomae and ephyrae and the strobilation dynamics of *Aurelia* populations collected from 17 locations around the world. Populations were from three species and we tested whether the same species assignments would be made using morphological measurements of scyphistomae and ephyrae. We also measured characteristics of strobilation (duration, number of ephyrae per scyphistoma), contrasting Pacific from Atlantic populations. We performed these comparisons not only to help clarify the taxonomic status of the genus but also to gain knowledge of basic features of scyphistomae and their reproductive dynamics in the laboratory.

Material and methods

Cultures

We compared the morphology of scyphistomae and ephyrae from populations of *Aurelia* collected at 17 locations in the North and Baltic Seas as well as the Atlantic and Pacific Oceans (Table 1). A priori species identifications were: populations 1 to 14 = *A. aurita*, populations 15 and 16 = *A. labiata*, and culture 17 = *A. limbata*. Species-level identifications were made *a priori* based on the morphology of medusae. Scyphistomae were kept in culture for more than 5 years. Scyphistomae and ephyrae were cultured using natural seawater at temperatures (SANYO incubators MIR 553 and MIR 253) and salinities (ATAGO S7Mill refractometer) that represented their local conditions (Table 1).

Scyphistomae were kept in 150-ml glass bowls in darkness and ephyrae were maintained in aerated, 500-ml flasks in daylight with the photoperiods occurring between May 5th and September 23rd 2009 in Hamburg, Germany, and room temperature (18 to 21°C). Based on previous work, we tried to induce strobilation by first decreasing the temperature and then raising it again to the initial temperature (Holst 2008, Holst 2012a). In 14 cultures (all except cultures 6 and 14 because strobilation was happening already on a regular basis) temperature was set from 15°C to 10°C and back to 15°C after 7 days. In

Table 1. Origin, salinity and incubation temperature of 17 different cultures of *Aurelia* sp. Strobilation was induced by temperature drop and, if required, additional potassium iodine (KI).

Culture	Proposed species (a priori)	Origin	Location	long /lat	Salinity (psu)	Temperature (°C)		
						Scyphistomae	Strobilation	Ephyrae
1	*A. aurita*	North Sea	Sylt, Germany	N 55°02'32" E 8°24'40"	34	10–15	10	Room temp (18–22°C)
2		North Sea	Helgoland, Germany	N 54°10'50" E 7°52'50"	34	10–15	10 (KI)	Room temp (18–22°C)
3		Northeast Atlantic	Hebrides, Scotland	N 57°36'01" W 7°0'01"	34	10–15		
4		Baltic Sea	Boiensdorf, Germany	N 54°01'57" E 11°33'16"	20	10–15		
5		Baltic Sea	Strande, Germany	N54°26'10" E10°10'21"	20	10–15		
6		East Atlantic	Roscoff, France	N48°43'40" W3°59'07"	34	15	15	Room temp (18–22°C)
7		Arctic Ocean	White Sea	N65°33'49" E36°36'33"	34	10–15		
8		North Sea/ Skagerrak	Kristineberg, Sweden	N58°14'59" E11°26'57"	34	10–15	10 (KI)	Room temp (18–22°C)
9		Mediterranean Sea	Cattolica, Italy	N43°58'14" E12°44'21"	34	15–23	15 (KI)	Room temp (18–22°C)
10		Red Sea	Gulf of Aqaba	N29°31'58" E34°58'18"	34	23		
11		West Atlantic	Woods Hole, USA	N41°31'34" W70°40'41"	34	10–15		
12		West Atlantic	Ilha Grande, Brazil	S23°06'00" W44°10'22"	34	23		
13		East Pacific	Monterey, USA	N36°36'50" W121°53'40"	34	10–15		
14		West Pacific	Kagoshima Bay, Japan	N31°30'08" E130°38'11"	34	15	15	Room temp (18–22°C)
15	*A. labiata*	East Pacific	Friday Harbor, USA	N48°29'42" W123°00'03"	34	10–15		
16		East Pacific	Coos Bay, USA	N43°23'00" W124°12'00"	34	10–15	10	Room temp (18–22°C)
17	*A. limbata*	Sea of Okhotsk, Pacific	Hokkaido, Japan	N44°10'10" E144°20'20"	34	10–15		

culture 9 temperature was set from 23°C to 15°C and back to 23°C after 7 days. Three out of the seven cultures in which strobilation actually occurred were additionally treated with potassium iodine (1.5 ml KI in 100 ml seawater; Spangenberg 1967, 1968) because the short-term temperature decrease was not sufficient to induce strobilation (Table 1). Scyphistomae and ephyrae were fed *Artemia salina* (Linné, 1758) nauplii once a week and every other day, respectively.

Morphological and statistical analyses

Scyphistomae

Scyphistomae were transferred to petri dishes and a 30-min period was allowed for them to relax and fully re-expand. Afterwards, individuals were digitally photographed and morphometric measurements were made using computer image analysis (ColorView, Soft Imaging System GmbH). Various morphological features were documented (colour, shape, number of tentacles) as well as strobilation duration and ephyrae production (Fig. 1). We took morphometric measurements as mentioned above following the method developed by Straehler-Pohl (2009), Straehler-Pohl & Jarms (2010) and Straehler-Pohl *et al.* (2011). The morphometric measurements of scyphistomae were compared by using the following ratios (expressed in percent; abbreviations are explained in Table 2): CL/TBL; HL/TBL; StL/TBL; MDD/TBL; CD0/CL; CD1/CL; CD2/CL; CD3/CL; StID/CL (for original data please refer to Appendix A).

Ephyrae

Ephyrae were measured within 24 h after detachment. They were collected from petri dishes using a pipette and transferred with a small amount of water to a glass slide with the manubrium facing up, where they where allowed to relax for 5–10 minutes. They were photographed and measured as described above for scyphistomae, including differences in rhopalial lappet- and gastric canal forms (Fig. 1D). We took morphometric measurements as mentioned above following the method developed by Straehler-Pohl (2009), Straehler-Pohl & Jarms (2010) and Straehler-Pohl *et al.* (2011). The morphometric measurements

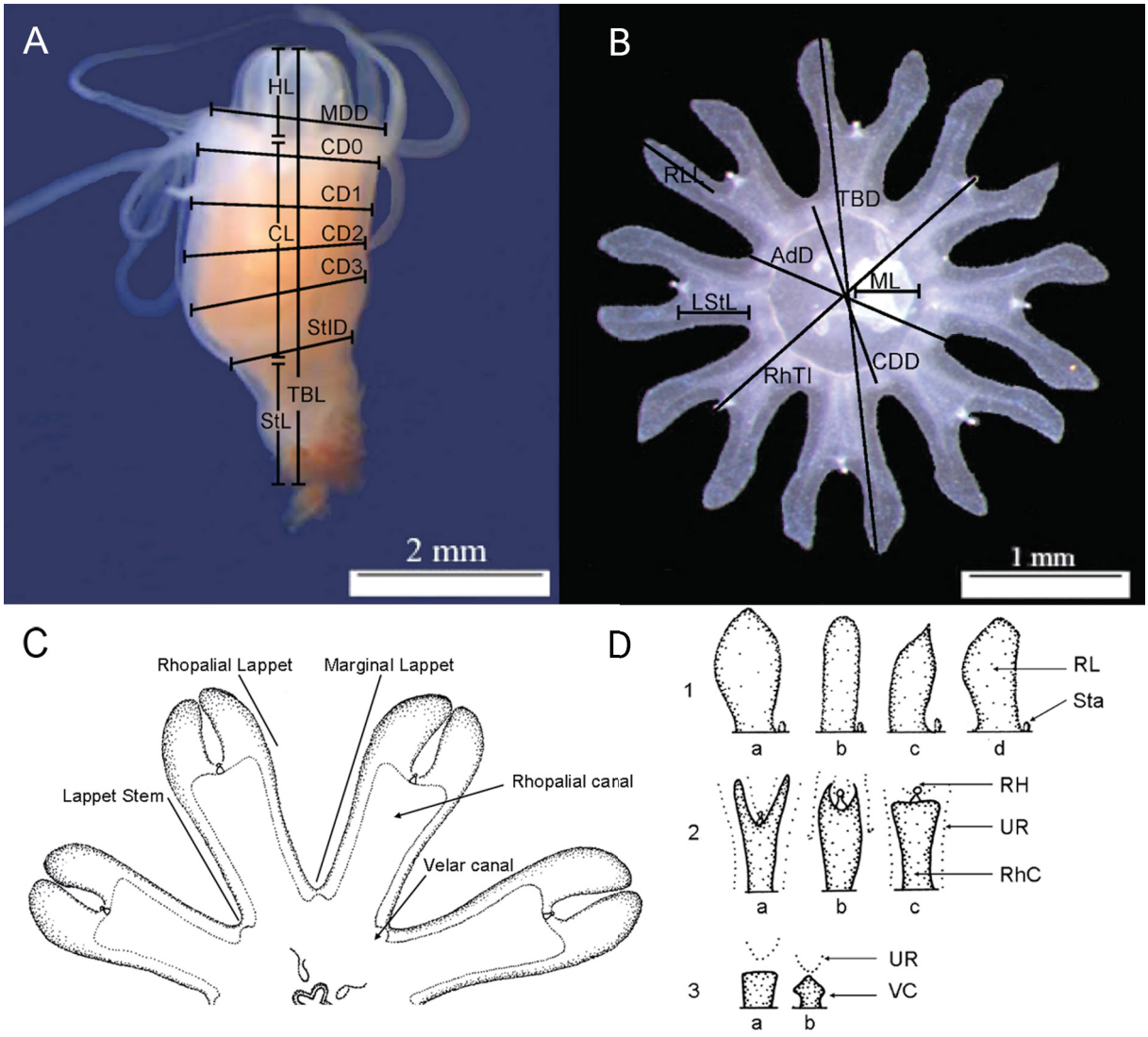


Fig. 1. Measurements of: **A**. Scyphistomae. **B**. Ephyrae. **C**. Lappets of an ephyra: the marginal lappet can be divided into rhopalial lappet and lappet stem; also visible are the rhopalial and velar canals. **D**. Rhopalial lappet and gastric canal forms of ephyrae in this study: **1**. Rhopalial lappet forms (i.e. left lappet): (a) pointed spoon-like, (b) round spatula-like, (c) lancet-like and (d) bread knife-like; **2**. Rhopalial canal forms: (a) forked, sharp points, (b) club-shaped, forked, sharp points and (c) spade-like; **3**. Velar canal forms: (a) spade-like and (b) rhombic. Abbreviations: RH = rhopalium; RhC = rhopalial canal; RL = rhopalial lappet; Sta = statolith; UR = umbrella rim; VC = velar canal. Other abbreviations: see Table 2. Modified after Straehler-Pohl & Jarms (2010).

Table 2. Measuring parameters for scyphistomae and ephyrae mainly according to Straehler-Pohl (2009), Straehler-Pohl & Jarms (2010) and Straehler-Pohl *et al.* (2011).

Abbreviations for scyphistomae	Actual measurement for scyphistomae
TBL (Total Body Length)	length from hypostome tip to basal disc
CL (Calyx Length)	length from gastric cavity base to tentacle crown rim
HL (Hypostome Length)	length from tentacle crown base to hypostome tip
MDD (Mouth Disc Diameter)	widest diameter of mouth disc
StL (Stalk Length)	length from basal disc to gastric cavity base
CD0–3 (Calyx Diameter)	diameter of the calyx at four different areas
StID (Stalk Initial Diameter)	diameter of the stalk at its beginning
Abbreviations for ephyrae	**Actual measurements for ephyrae**
TBD (Total Body Diameter)	2x total length of marginal lappet + diameter of central disc
CDD (Central Disc Diameter)	diameter of the central disc from the end of the gastric cavity
TMLL (Total Marginal/Rhopalial Lappet Length)	length of the lappet stem + length of rhopalial lappet
LStL (Lappet Stem Length)	length from lappet base (line between the bases of two marginal lappet clefts) to base of rhopalial niche (base of cleft between two rhopalial lappets)
RLL (Rhopalial Lappet Length)	length from rhopalial niche base to level of rhopalial lappet tips
ML (Manubrium Length)	length between base and rim of manubrium
AdD (Adradial Diameter)	adradial diameter of the central disc
RhTI (Rhopalar Tip Interspace)	space between the rhopalar tips

of ephyrae were compared by using the following ratios (expressed in percent; abbreviations are given in Table 2): LStL/TMLL; RLL/TMLL; CDD/TBD; ML/TBD; RhTI/TBD; AdD/TBD; CDD/AdD; ML/AdD; TMLL/TBD; LStL/TBD; RLL/TBD (for original data please see Appendix B).

We explored statistically significant differences between the 17 populations using a post-hoc, stepwise Linear Discriminant Analysis (LDA) of the ratios based on the morphometric measurements (n = 6 individuals per population). Ephyra production and number of tentacles per scyphistoma (both n = 10) were evaluated using a Kruskal-Wallis test, followed by a Tukey's Honestly Significant Difference (HSD) post-hoc test. The significance level was set at alpha < 0.05. Statistical analyses were performed using the software R 2.15.2 (R Core Team 2012).

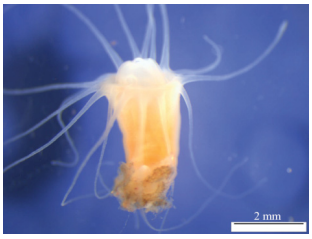
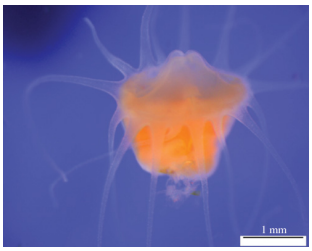
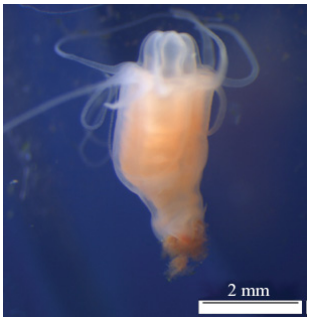
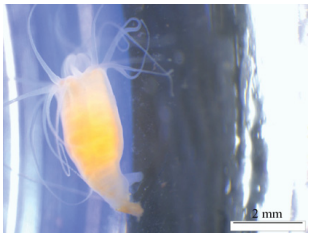
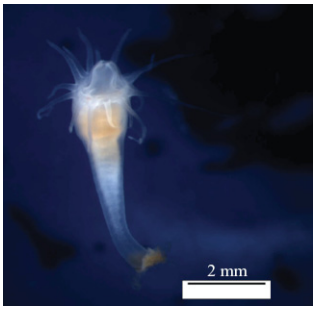
Results

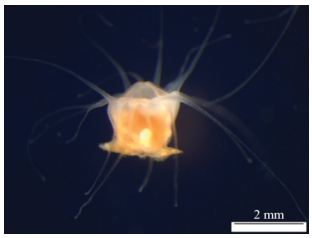
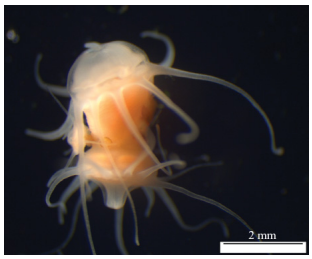
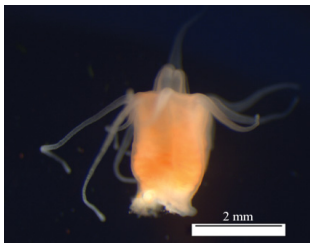
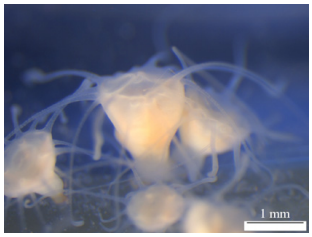
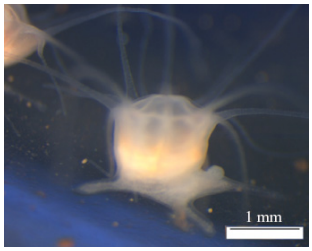
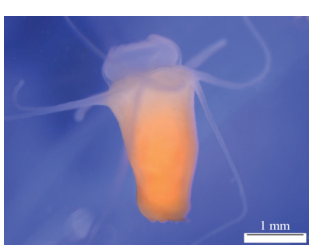
Morphological analyses

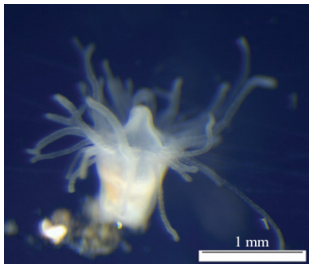
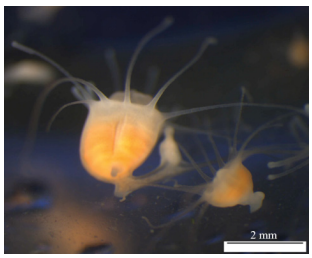
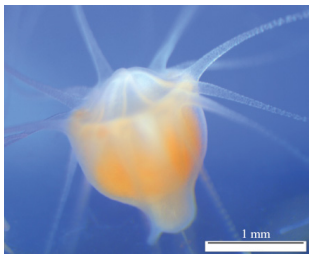
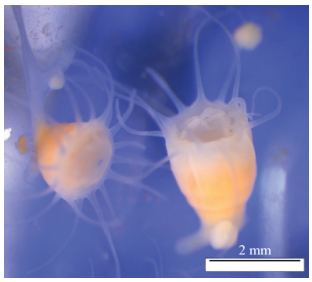
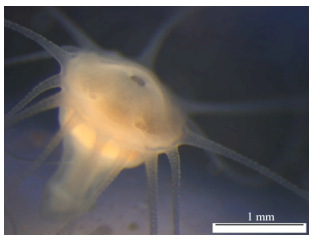
Scyphistomae

Scyphistomae of the 17 *Aurelia* populations were morphologically variable with respect to colour and shape of the calyx, the shape of the hypostome, and the number of tentacles (Table 3). We were able to distinguish four different calyx shapes (barrel, square, chalice, and cone) and four different hypostome shapes (convex, cap, cylindrical, and cone). The number of tentacles varied significantly among the populations (Kruskal-Wallis, $H_{16} = 67.3$, $p > 0.00001$, n = 10). Pairwise comparison revealed that population 12 (West Atlantic) was significantly different from all others (HSD, $p \leq 0.05$). In 10 of the 17 populations there was a consistent ranking of body proportion (CL > HL > StL) and stalks in populations 4–6 (Baltic Sea and East Atlantic), 9 (Mediterranean Sea), 13 (East Pacific), 15 (East Pacific) and 16 (East Pacific) were longer than the hypostome (CL > StL > HL; Fig. 2). There were significant differences between ratios of hypostome length, calyx length and stem length in relation to

Table 3. Collected morphological features of the scyphistomae of *Aurelia* sp.; tentacles were counted on 10 individuals

Polyp types	Culture	Calyx shape	Calyx colour	Hypostome shape	Number of tentacles (N=10)
	1	barrel-like	orange	convex	15.8 ± 0.79
	2	square, jolted	orange	cap-like	15.9 ± 0.32
	3	barrel-like, offset stalk	orange	cylindrical	16.2 ± 0.42
	4	barrel-like, offset stalk	orange in the middle, rest milky white	cylindrical	15.9 ± 0.57
	5	chalice-like, long stem	little orange in the middle, rest milky white	cylindrical	15.9 ± 0.57

Polyp types	Culture	Calyx shape	Calyx colour	Hypostome shape	Number of tentacles (N=10)
	6	square	orange	cone-shaped	15.9 ± 0.32
	7	barrel-like	orange	convex	15.5 ± 0.71
	8	barrel-like	orange	cylindrical	15.8 ± 0.42
	9	cone-like	milky white	cone-shaped	16.2 ± 0.42
	10	square	milky white	barely convex	16.2 ± 0.63
	11	barrel-like	orange	convex, large	16.0 ± 0

Polyp types	Culture	Calyx shape	Calyx colour	Hypostome shape	Number of tentacles (N=10)
	12	cone-like, slender	milky white	cap-like	28.8 ± 2.6
	13	chalice-like	orange in calyx, milky white around mouth disc and tentacles	cone-shaped	16.1 ± 0.32
	14	chalice-like	orange in calyx, milky white around mouth disc and tentacles	cone-shaped	16.0 ± 0
	15	chalice-like	orange in calyx, milky white around mouth disc and tentacles	cone-shaped	15.9 ± 0.74
	16	chalice-like	light orange	cone-shaped	16.0 ± 0
	17	chalice-like	orange in calyx, milky white around mouth disc and tentacles	cylindrical	16.2 ± 0.63

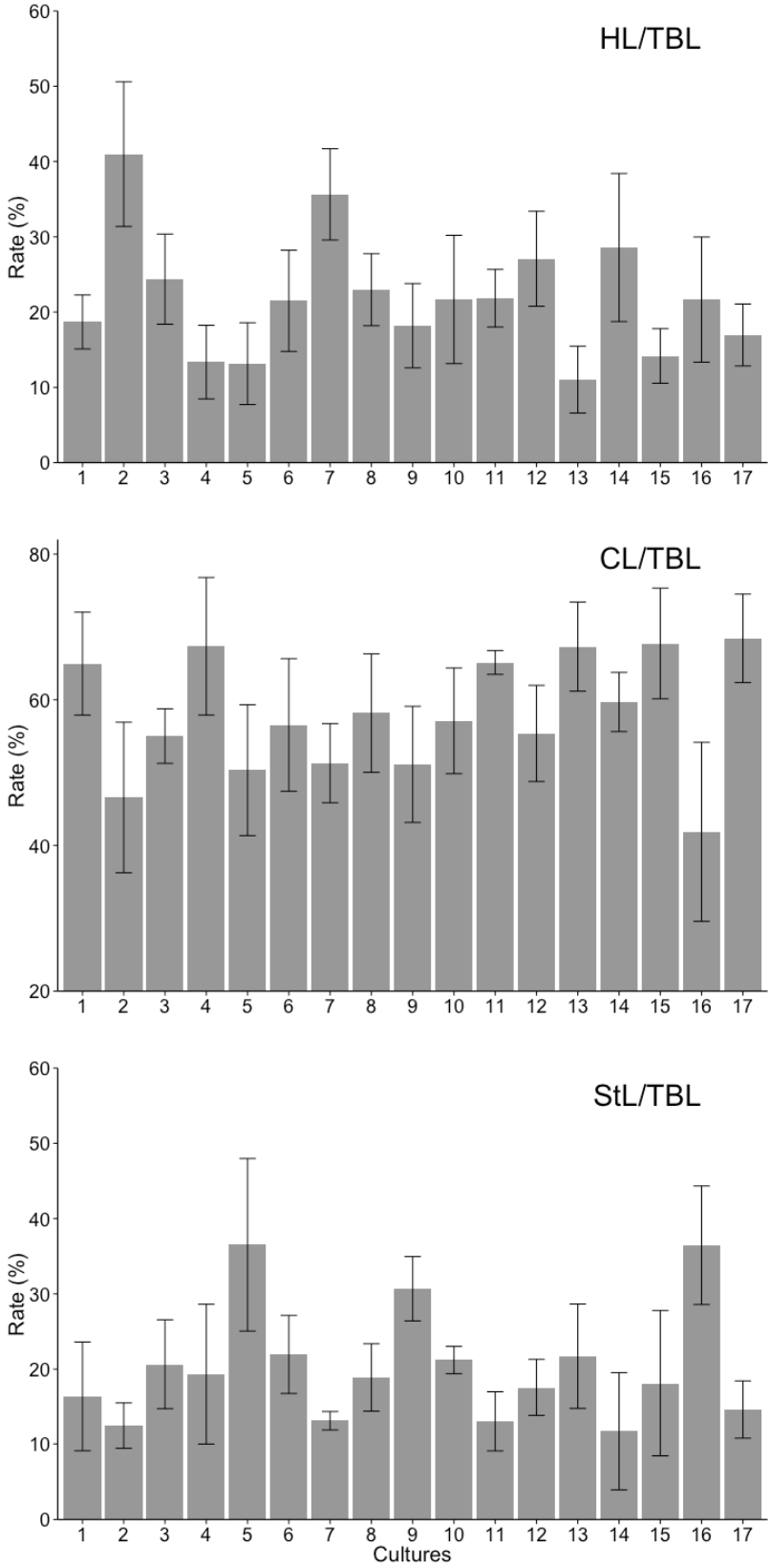


Fig. 2. Body proportions of polpys (shown as percentage). Error Bars show standard deviation. Abbreviations: see Table 2.

Table 4. Analysis of Variances (ANOVA) for morphometric indices of scyphistomae and ephyrae. Abbreviations: df = degrees of freedom; F = F-Ratio; p = p-Value. Other abbreviations: see Table 2

Comparison of scyphistomae	**dF**	**F**	**p**	***
CL/TBL	16, 88	9.88	< 0.001	***
HL/TBL	16, 88	9.87	< 0.001	***
StL/TBL	16, 88	8.71	< 0.001	***
Comparison of ephyrae	**dF**	**F**	**p**	***
RLL/TBD	6, 35	16.17	< 0.001	***
ML/TBD	6, 35	6.98	< 0.001	***
TMLL/TBD	6, 35	24.73	< 0.001	***
LStL/TBD	6, 35	26.70	< 0.001	***
CDD/TBD	6, 35	39.63	< 0.001	***
RLL/TMLL	6, 35	16.87	< 0.001	***
LStL/TMLL	6, 35	16.87	< 0.001	***
RhTI/TBD	6, 35	8.69	< 0.001	***

total body length of scyphistomae (ANOVA, $p < 0.001$, Fig. 2, Table 4). Most of the scyphistomae had 14 to 17 tentacles except cultures 15 and 16 (14 to 16) and culture 12 (27 to 33).

Strobilation

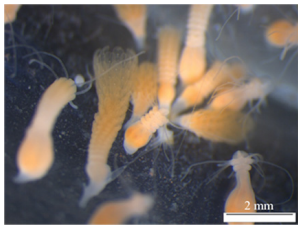
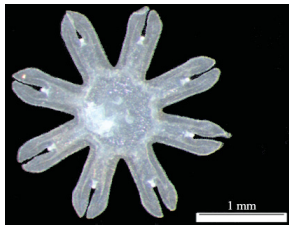
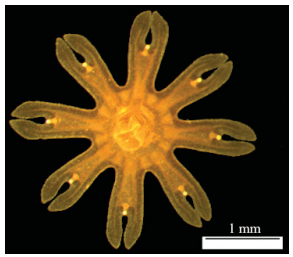
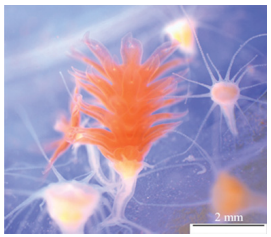
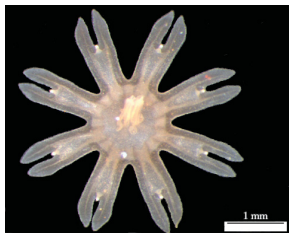
Strobilation occurred in 7 of the 17 populations (Tables 1, 5). In cultures 1 (North Sea) and 16 (East Pacific), scyphistomae strobilated after a decrease in temperature. In cultures 2 (North Sea), 8 (North Sea / Skagerrak) and 9 (Mediterranean Sea), strobilation commenced after exposure to KI and a decrease in temperature. Cultures 6 (East Atlantic) and 14 (Pacific) were maintained at 15°C and strobilated several times. The strobilation process from the development of the first constriction until detachment of the last ephyra lasted 17 to 27 days. In six of seven cultures, at least ten scyphistomae strobilated. Only 1 scyphistoma strobilated in culture 1 (North Sea) and this culture was not included in further analyses concerning the strobilation process. Cultures from the Pacific Ocean (cultures 14 and 16) had much shorter strobilation times (17 to 18 days) compared to the four cultures from the East Atlantic Ocean / North Sea (cultures 1, 2, 6 and 8) and the Mediterranean (culture 9). In these six cultures (i.e., excluding culture 1), the mean (± standard deviation) number of ephyrae per strobila varied from 6.0 ± 0.9 to 21.1 ± 3.0 and was significantly different among cultures (Kruskal-Wallis $H5 = 47.4$, $p < 0.001$, $n = 10$). The number of ephyrae per strobila in the Pacific cultures was significantly lower than that of the remaining experimental cultures (HSD, $p \leq 0.05$).

Ephyrae

The colour of the ephyrae ranged from translucent white to translucent pink to reddish brown (Table 5). The shape of the rhopalial lappets as well as the shapes of the rhopalial and velar canals differed between cultures (Table 5). Lappet proportions of the ephyrae exhibited differences. Culture 6 (East Atlantic) produced ephyrae showing ratios of rhopalial lappet (RLL) to lappet stem length (LStL) of almost 60% whereas others were about 50% (Fig. 3). A factorial ANOVA revealed significant differences of body proportions between all species ($p < 0.001$, Fig. 3, Table 4).

Table 5. Collected morphological features of the ephyrae of *Aurelia* sp.

Strobila type	Ephyra type	Culture	Induction / duration (days) of strobilation	Ephyrae per Strobila (N = 10, p < 0.05)	Significantly different from	Ephyra colour	Rhopalial lappet form	Rhopalial canal form	Velar canal form
		1	temperature drop / 24	14		translucent pink	pointed spoon-like	spade-like	rhombic
		2	temperature drop and KI / 25	21.1 ± 2.96*	6, 9, 14, 16	whitish yellow	lancet-like	forked, sharp points	rhombic
		6	autonomous strobilation / 21	15.6 ± 1.6*	14, 16	reddish brown	bread knife-like	spade-like	spade-like
		8	temperature drop and KI / 25	15.1 ± 3.9*	14, 16	white translucent	round spatula-like	spade-like	rhombic

Strobila type	Ephyra type	Culture	Induction / duration (days) of strobilation	Ephyrae per Strobila (N = 10, p < 0.05)	Significantly different from	Ephyra colour	Rhopalial lappet form	Rhopalial canal form	Velar canal form
		9	temperature drop and KI / 27	17.1 ± 3.5*	2, 14, 16	white yellow	bread knife-like	club-shaped, forked	spade-like
		14	autonomous strobilation / 17	6.0 ± 0.9*	2, 6, 8, 9	reddish brown	bread knife-like	spade-like	spade-like
		16	temperature drop / 18	7.0 ± 0.9*	2, 6, 8, 9	reddish brown	bread knife-like	spade-like	spade-like

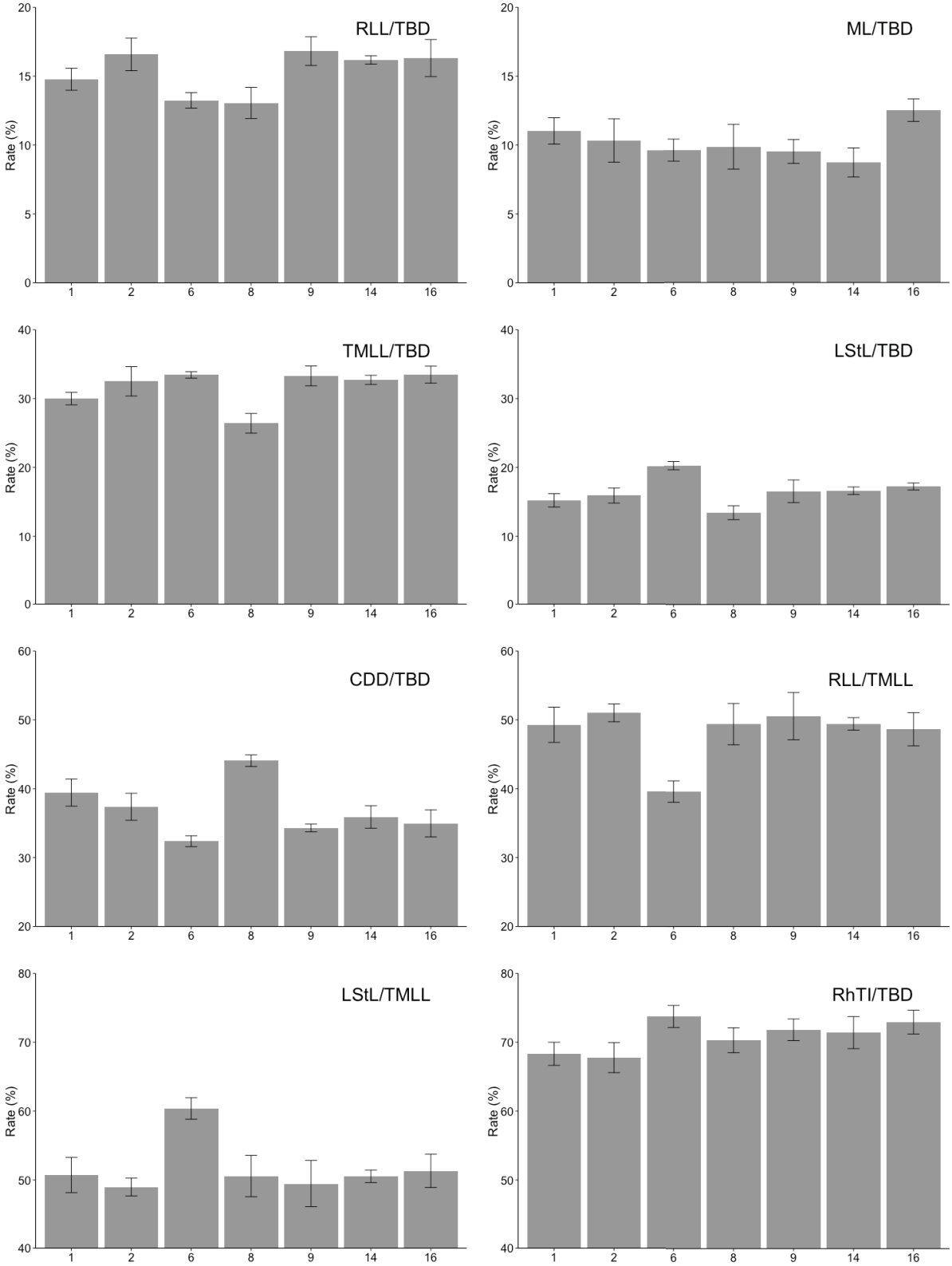


Fig. 3. Body proportions of ephyrae (shown as percentages). Error bars show standard deviation. Abbreviations: see Table 2.

Linear Discriminant Analysis (LDA)

Scyphistomae

The LDA based on ratios of morphometric measurements for scyphistomae did not identify any kind of separation among the 17 populations. All populations overlapped to varying degrees except for populations 2 (North Sea) and 16 (East Pacific; Fig. 4A).

Ephyrae

The LDA based on ratios of morphometric measurements for ephyrae suggested distinct classifications (Fig. 4B) with overlaps between populations 9 (Mediterranean Sea) and 14 (Pacific), 1 and 2 (North Sea), and a similar placement of populations 16 (East Pacific) and 9 (Mediterranean Sea). Ephyrae from populations 6 (East Atlantic) and 8 (North Sea / Skagerrak) were completely isolated from each other and from the other populations.

Discussion

Some morphological features of scyphistomae and ephyrae can be used to distinguish congeners while others cannot. Straehler-Pohl & Jarms (2010) reported that the relation between rhoparlar lappet length (RLL) and lappet stem length (LStL) and the development of the gastric system could be important distinguishing features of genera but not species. *Aurelia aurita* from the North Sea has rhopalial (forked, sharp points) and velar canals (rhombic) as well as lancet-like rhopalial lappets (Straehler-Pohl & Jarms 2010; Straehler-Pohl *et al.* 2011; Holst 2012b), which match ephyrae from population 2. In this study, ephyrae have four different rhopalial lappet shapes, three different rhopalial canal shapes and two different velar canal shapes, which supports the genetic evidence suggesting more than three species within *Aurelia* (Dawson & Jacobs 2001; Dawson & Martin 2001; Schroth *et al.* 2002). Although colour is another trait that depends on a variety of factors, when maintained on the same diet (*Artemia* nauplii),

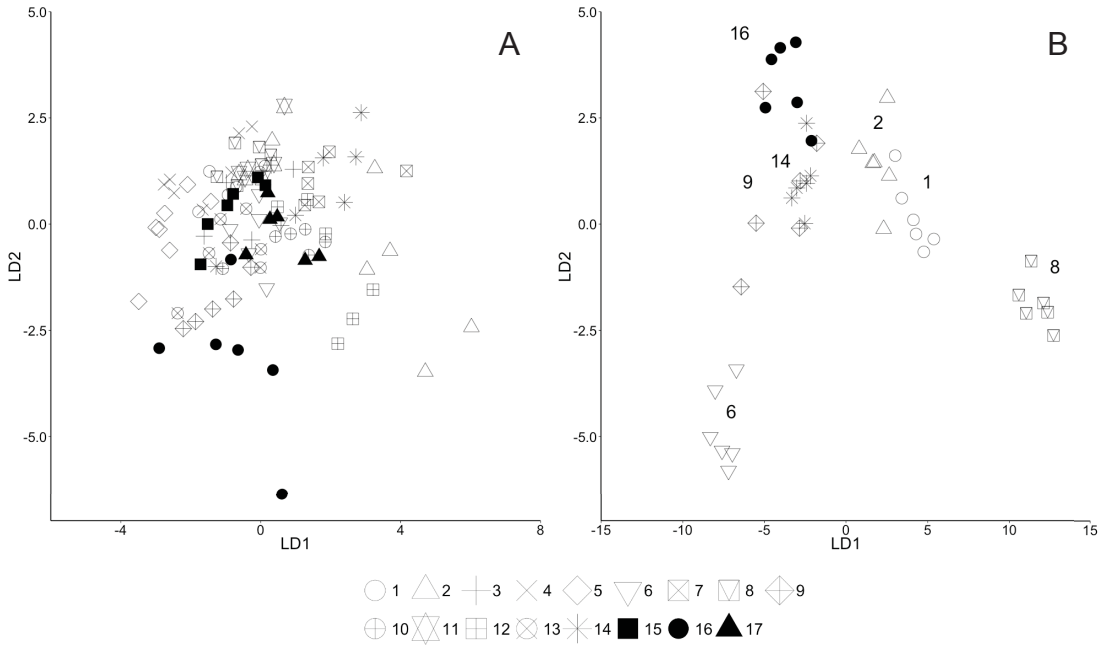


Fig. 4. Linear Discriminant Analysis based on the morphology. **A**. Scyphistomae (17 cultures) of *Aurelia* congeners. **B**. Ephyrae (7 of the 17 cultures) of *Aurelia* congeners. In each case, cultures can be distinguished from one another by different symbols and corresponding numbers (see legend).

higher latitude scyphistomae produce white and translucent ephyrae and the degree of pigmentation increased with decreasing latitude. Moreover, ephyrae produced by Pacific scyphistomae differed in colour from those produced by scyphistomae collected from the Atlantic Ocean and Mediterranean Sea. Therefore, colour can be a useful trait if compared among individuals maintained using the same culture/feeding conditions.

The LDA we conducted using the morphometric data of ephyrae reveal a clear separation of the different populations (Fig. 4b), which again supports the genetically indicated existence of more than three species. The obvious partitioning clearly allows classifications to be made and these are discussed (below) in light of known differences among the 17 populations.

In scyphistomae the colour of the calyx was not a reliable characteristic to differentiate among species, since it was more or less the same in all scyphistomae. We expected differences similar to the ones found in ephyrae, due to the same feeding conditions (Straehler-Pohl 2009; Straehler-Pohl & Jarms 2010; Holst 2012b). The shape of the calyx was a suitable character for separating species (e.g., a cup-like calyx is characteristic of *A. limbata* [Straehler-Pohl 2009; this study]), although the morphology of the calyx and hypostome can vary and can be misinterpreted (Berrill 1949; Straehler-Pohl 2009; Straehler-Pohl *et al.* 2011). Moreover, biotic and abiotic factors such as food intake, light intensity, salinity and temperature may affect the shape and colour of these features (Spangenberg 1964; Willcox *et al.* 2007). The number of tentacles is an obvious morphological feature of scyphistomae which also displays interspecific variability, with *A. aurita* and *A. labiata* having 14 to 28 (Holst 2008; Straehler-Pohl 2009; this study) and 14 to 21 (Gershwin 2001; Widmer 2006; this study), respectively. Scyphistomae of population 12 had between 27 and 33 tentacles and, based on this morphology, may not belong to *Aurelia*. Finally, the length of the hypostome in relation to the stem has been reported to distinguish members of Scyphozoa (Semaeostomeae: CL > HL > StL, Cepheida: StL > CL > HL, Rhizostomida: CL > StL > HL; Straehler-Pohl 2009; Straehler-Pohl *et al.* 2011). In this study, StL was > HL in only 40% of the specimens; this relationship is not suitable for distinguishing *Aurelia* congeners. Furthermore, we demonstrate that morphometric measurements of scyphistomae cannot be used to distinguish among species within this genus (Fig. 4A).

Lucas *et al.* (2012) provide a review of studies conducted on scyphistoma populations, including the species-specific triggers for strobilation. We were able to induce strobilation in 7 of the 17 populations using cues known to be effective for *Aurelia* species, including a decrease in temperature and, in some cases, the addition of KI (Berrill 1949; Spangenberg 1967; see Lucas *et al.* 2012). Spangenberg (1964) discovered that scyphistomae with large calices produce more ephyrae than small scyphistomae and still have enough energy to regenerate the residuum (Straehler-Pohl & Jarms 2005). Scyphistomae are often larger when grown at low salinities and low temperatures (Schroth *et al.* 2002; Willcox *et al.* 2007) and could therefore produce more ephyrae than smaller scyphistomae in warmer waters, possibly due to higher availability of tissue. Our results suggested longer durations of strobilation and greater numbers of ephyrae produced by scyphistomae collected from higher (colder) versus lower (warmer) latitudes despite scyphistomae being maintained at the same temperature in the laboratory, even though some populations needed the temperature drop and the consequent rise to start the strobilation process. Naturally, the number of ephyrae produced by scyphistomae depends upon both endogenous and exogenous factors (Lucas *et al.* 2012) and the effect of the latter make it difficult to use this trait to differentiate species within one genus.

Classification

Historical reports and descriptions of species within *Aurelia* often used geographical distribution as a distinguishing characteristic. However, geographical distributions of many planktonic organisms have changed via transport in ballast waters and jellyfish introductions are commonly reported (Greenberg

et al. 1996; Purcell *et al.* 2007). The potential for mixing of different (potentially cryptic) species within the same area demands that methods be found to reliably identify species. In the following, we discuss the 17 populations in terms of the results of our morphological observations of scyphistomae and ephyrae, morphometric measurements of ephyrae, recent genetic analyses as well as information on geographical distribution.

Group 1

Populations 1–5, 7, 8: Agreement - *A. aurita*. All of these scyphistomae were collected from eastern parts of the Atlantic Ocean and the Baltic Sea. Molecular (Dawson & Jacobs 2001; Schroth *et al.* 2002; Dawson *et al.* 2005), distributional (Mayer 1910, 1917; Kramp 1961; Russell 1970) and our data as described in Table 3 support this species identification for populations 1–5, 7 and 8. The effects of changes in salinity on the morphological characteristics of scyphistomae and ephyrae are not known and could influence classification based merely on morphology. However, morphometric measurements of ephyrae (see Table 5) suggested that population 8 was morphologically distinct from populations 1 and 2. We speculate that populations 1 and 8 may be boreal species as suggested by Schroth *et al.* (2002). The results of the LDA suggest that population 8 may be transitional between North Sea and Atlantic populations, which is supported by the findings of Dawson *et al.* (2005). Group 1 is considered to be a member to the initially described species, *Aurelia aurita* (Table 6).

Group 2

Population 6: Disagreement - *Aurelia aurita* which is likely another species. Scyphistomae in populations 6, 9 and 10 originated from geographically separate areas (North Sea, the Atlantic Ocean and Red Sea, respectively); nevertheless their scyphistomae and ephyrae share some common morphological characteristics (see Tables 3, 5). Unlike the genetic analyses reported by Schroth *et al.* (2002), our morphometric measurements distinguish population 6 from all the other groups. Dawson & Jacobs (2001) as well as Schroth *et al.* (2002) propose populations 6 and 14 to be the same species, and geographic differences may not be valid given ballast water transport of conspecifics. Still, based on the literature (Mayer 1910, 1917; Kramp 1961; Russell 1970) and our measurements, we suggest that population 6 represents the only member of group 2 and a new species, *Aurelia* sp. 1 (Table 6).

Group 3

Population 9: Disagreement – *A. aurita* which is likely another species. Animals from culture 9 were collected in the Mediterranean Sea and the separation into a new species is supported by genetic uniqueness (Dawson & Jacobs 2001; Dawson & Martin 2001; Schroth *et al.* 2002, Dawson *et al.* 2005). Also, the morphology of the ephyrae shows unique features, e.g., the yellowish colour in combination with the shape of the lappets and the shapes of rhopalial- and velar canals. Nonetheless, population 9 displays similar morphological features to *A. aurita* (Kramp 1961). Schroth *et al.* (2002) suggested a transitional habitat called "Tethys," which includes populations in the Mediterranean and Red Seas. We therefore provisionally place culture 9 within the taxon *Aurelia cruciata* Haeckel, 1880 (Mayer 1910; Kramp 1961) as it is located within the "Tethys" habitat.

Group 4

Population 10: Disagreement – *A. aurita* which is likely another species. Animals from population 10 were collected from the Gulf of Aqaba, also within this "Tethys" region defined by Schroth *et al.* (2002) and Dawson *et al.* (2005). Individuals display a similar morphology to *A. aurita* (Kramp 1961). We suggest placing population 10 within the taxon *Aurelia maldivensis* Bigelow, 1904 (Stiansy 1938; Kramp 1961) considering its range of distribution within the "Tethys" habitat (see Table 6).

Table 6. Classification of the different populations (cultures 1–17) into eight different groups/species based on our results (morphological and statistical: Linear Discriminant Analysis [LDA]) under consideration of the literature (genetic and distributional data).

Culture	Origin	Proposed species (a priori)	Was it the proposed species?	Suggested species	Group
1	North Sea	*Aurelia aurita*	yes	*Aurelia aurita*	1
2	North Sea		yes	*Aurelia aurita*	1
3	North Sea		yes	*Aurelia aurita*	1
4	Baltic Sea		yes	*Aurelia aurita*	1
5	Baltic Sea		yes	*Aurelia aurita*	1
6	East Atlantic		no	*Aurelia* sp. 1	2
7	Arctic Ocean		yes	*Aurelia aurita*	1
8	East Atlantic		yes	*Aurelia aurita*	1
9	Mediterranean Sea		no	*Aurelia cruciata*	3
10	Red Sea		no	*Aurelia maldivensis*	4
11	West Atlantic		no	*Aurelia flavidula*	5
12	West Atlantic		no	*Aurelia* sp. 2	6
13	East Pacific		no	*Aurelia labiata*	7
14	Pacific		no	*Aurelia labiata*	7
15	East Pacific	*Aurelia labiata*	yes	*Aurelia labiata*	7
16	East Pacific		yes	*Aurelia labiata*	7
17	Pacific	*Aurelia limbata*	yes	*Aurelia limbata*	8

Group 5

Population 11: Disagreement - *Aurelia aurita* which is likely another, transitional species. Based on known distributions of adult medusae (given the caveats of potential mixing) and morphological features (Table 5), population 11 can be separated from the other Atlantic populations of *A. aurita*. This population is possibly a member of the taxon *Aurelia flavidula* Péron & Lesueur, 1809 (Péron & Lesueur 1809; Mayer 1910; Kramp 1961) or *Aurelia marginalis* Agassiz, 1862 (Mayer 1910). Classification into a different taxon seems reasonable at this point, even though these findings are not yet supported by molecular data.

Group 6

Population 12: Disagreement – *A. aurita* which is likely another species. Collected from Brazilian waters, the morphology of scyphistomae (27–33 tentacles) of population 12 differs from all other populations. The shape of the calyx in combination with the cap-like hypostome, as well as the very small size of the scyphistomae, suggest differences from the other populations. Dawson & Jacobs (2001) found an *Aurelia* species on the east coast of South America that also has a unique morphology. Mayer (1910) described individuals off the Brazilian coast as *A. aurita*. Either there have been some misclassifications or both

species coexist in this area. Based on the results of this study and the currently available literature, we suggest this population to be a separate species, which we call *Aurelia* sp. 2.

Group 7

Populations 13–16: Agreement – *A. labiata*. Both genetic analyses and morphological observations of scyphistomae, strobilae and ephyrae and morphometric measurements in ephyrae correctly distinguished populations 13–16 as *A. labiata* (Gershwin 2001; Dawson & Jacobs 2001; Dawson *et al.* 2005; Widmer 2005). The genetic relationship between populations 16 and 6 as reported by Schroth *et al.* (2002) cannot be substantiated. Genetic analyses classify US west coast populations of *Aurelia* as *A. labiata* (Dawson & Jacobs 2001; Dawson & Martin 2001; Schroth *et al.* 2002) and the morphology of both ephyrae and adult medusae (Mayer 1910; Gershwin 2001; Dawson 2003; Widmer 2005) support this classification. Nevertheless, differences in morphology and life cycle suggest that southern, central and northern varieties exist (Gershwin 2001) or that these may represent different species (Dawson 2003).

Group 8

Population 17: Agreement – *A. limbata*. Our morphological observations of these scyphistomae match those previously made by Uchida & Nagao (1963) and the species is confirmed by both morphological (Kramp 1961) and genetic features (Dawson & Martin 2001; Schoth *et al.* 2002, Dawson *et al.* 2005) of medusae. *Aurelia limbata* is found in the Northwest and Northeast Pacific, northern Japan, Western Greenland, Alaska, Labrador and Siberia (Mayer 1910; Bigelow 1913; Uchida 1934; Kramp 1961).

Conclusion

We provide a detailed morphological dataset for the scyphistomae of 17 populations of *Aurelia* congeners. Morphometric characteristics of ephyrae from 7 populations were good indicators of different species/groups; still, morphometric data of scyphistomae collected and processed by the method of Straehler-Pohl (2009), Straehler-Pohl & Jarms (2010) and Straehler-Pohl *et al.* (2011) where not separative in order to distinguish among *Aurelia* species. Based on morphological differences (this study), genetic differences (Dawson & Jacobs 2001; Dawson & Martin 2001; Schroth *et al.* 2002; Dawson 2003; Dawson *et al.* 2005) and differences in geographical distribution (Mayer 1910; Kramp 1961; Russell 1970; Gershwin 2001; Widmer 2005), we suggest a separation of these 17 populations, which would include 8 groups: *A. aurita*, *A. labiata*, *A. limbata*, two new *Aurelia* spp., and three formerly recognized species. Our assessments agree with the *a priori* species assignments for 10 of the 17 populations. This is another step towards understanding the complexity of the genus *Aurelia* and it reveals the importance of considering the whole cnidarian life cycle, particularly differences in asexual propagation and morphological characteristics of ephyrae, when attempting to distinguish species.

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Appendix A. Morphological measurements of scyphistomae (mean ± sd) in mm.

Culture	TBL	CL	HL	MDD	StL	CD0	CD1	CD2	CD3	StID
1	4.11 ± 0.30	2.67 ± 0.33	0.77 ± 0.14	1.98 ± 0.24	0.68 ± 0.30	1.79 ±0.14	1.71 ± 0.09	1.61 ± 0.10	1.49 ± 0.25	0.50 ± 0.23
2	2.82 ± 0.73	1.35 ± 0.65	1.11 ± 0.18	2.40 ± 0.27	0.35 ± 0.13	2.35 ± 0.26	2.15 ± 0.29	1.93 ± 0.36	1.60 ± 0.40	0.51 ± 0.25
3	3.85 ± 0.67	2.11 ± 0.31	0.93 ± 0.25	2.15 ± 0.33	0.82 ± 0.34	2.14 ± 0.39	2.03 ± 0.34	1.85 ± 0.39	1.58 ± 0.34	0.54 ± 0.06
4	5.23 ± 0.45	3.52 ± 0.56	0.69 ± 0.22	1.73 ± 0.17	1.02 ± 0.55	1.79 ± 0.22	1.78 ± 0.23	1.80 ± 0.44	1.74 ± 0.46	0.50 ± 0.11
5	4.30 ± 0.52	2.18 ± 0.54	0.55 ± 0.20	1.69 ± 0.18	1.57 ± 0.53	1.64 ± 0.19	1.59 ± 0.27	1.55 ± 0.31	1.30 ± 0.26	0.24 ± 0.05
6	2.89 ± 0.34	1.64 ± 0.35	0.62 ± 0.20	1.85 ± 0.16	0.63 ± 0.16	1.89 ±0.31	1.72 ±0.36	1.50 ± 0.35	1.28 ± 0.34	0.40 ± 0.13
7	2.87 ± 0.35	1.47 ± 0.23	1.03 ± 0.21	1.95 ± 0.22	0.37 ± 0.04	1.93 ± 0.16	1.77 ± 0.18	1.65 ± 0.17	1.40 ± 0.20	0.50 ± 0.18
8	3.46 ± 0.32	2.00 ± 0.25	0.80 ± 0.22	1.61 ± 0.20	0.66 ± 0.19	1.78 ± 0.24	1.79 ± 0.29	1.66 ± 0.31	1.41 ± 0.32	0.50 ± 0.08
9	2.22 ± 0.15	1.13 ± 0.14	0.41 ± 0.14	1.52 ± 0.05	0.69 ± 0.14	1.43 ± 0.18	1.34 ± 0.18	1.11 ± 0.27	0.87 ± 0.28	0.32 ± 0.10
10	1.89 ± 0.19	1.08 ± 0.20	0.41 ± 0.16	1.48 ± 0.07	0.40 ± 0.07	1.52 ± 0.11	1.55 ± 0.14	1.43 ± 0.14	1.15 ± 0.19	0.29 ±0.06
11	3.25 ± 0.31	2.11 ± 0.19	0.71 ± 0.11	1.57 ± 0.07	0.43 ± 0.16	1.54 ± 0.08	1.35 ± 0.11	1.35 ± 0.10	1.32 ± 0.16	0.39 ± 0.07
12	1.18 ± 0.26	0.66 ± 0.23	0.31 ± 0.08	1.01 ± 0.11	0.20 ± 0.04	1.05 ± 0.18	0.95 ± 0.15	0.83 ± 0.17	0.66 ± 0.17	0.24 ± 0.09
13	3.36 ± 0.42	2.25 ± 0.22	0.37 ± 0.14	2.00 ± 0.27	0.75 ± 0.31	1.91 ± 0.21	1.67 ± 0.21	1.53 ± 0.17	1.27 ± 0.15	0.38 ± 0.14
14	2.02 ± 0.33	1.21 ± 0.25	0.55 ± 0.16	1.38 ± 0.15	0.25 ± 0.22	1.37 ± 0.15	1.22 ± 0.14	1.16 ± 0.15	1.03 ± 0.22	0.20 ± 0.05
15	3.67 ± 0.52	2.47 ± 0.38	0.51 ± 0.06	1.89 ± 0.24	0.69 ± 0.44	1.89 ± 0.38	1.81 ± 0.32	1.65 ± 0.25	1.32 ± 0.21	0.47 ± 0.06
16	2.26 ± 0.34	0.96 ± 0.36	0.48 ± 0.18	1.54 ± 0.06	0.82 ± 0.20	1.39 ± 0.05	1.16 ± 0.06	0.93 ± 0.10	0.71 ± 0.06	0.24 ± 0.02
17	2.76 ± 0.32	1.90 ± 0.33	0.46 ± 0.08	2.09 ± 0.15	0.41 ± 0.12	2.13 ± 0.17	2.11 ± 0.16	1.93 ± 0.24	1.52 ± 0.35	0.45 ± 0.15

Appendix B. Morphological measurements of ephyrae (mean ± sd) in mm.

Culture	TBD	CDD	TMLL	LStL	RLL	ML	AdD	RhTI
1	3.44 ± 0.23	1.36 ± 0.13	1.03 ± 0.06	0.52 ± 0.02	0.51 ± 0.05	0.38 ± 0.05	1.45 ± 0.13	2.34 ± 0.18
2	3.54 ± 0.32	1.32 ± 0.10	1.15 ± 0.10	0.56 ± 0.04	0.59 ± 0.06	0.37 ± 0.06	1.43 ± 0.10	2.40 ± 0.18
6	3.27 ±0.12	1.06 ± 0.03	1.09 ± 0.05	0.66 ± 0.03	0.43 ± 0.03	0.32 ± 0.03	1.21 ± 0.02	2.41 ± 0.06
8	2.92 ± 0.09	1.29 ± 0.04	0.77 ± 0.04	0.39 ± 0.03	0.38 ± 0.04	0.29 ± 0.05	1.38 ± 0.03	2.05 ± 0.02
9	2.76 ± 0.21	0.95 ± 0.07	0.92 ± 0.08	0.46 ± 0.06	0.46 ± 0.03	0.26 ± 0.02	1.05 ± 0.07	1.98 ± 0.19
14	3.37 ± 0.11	1.21 ± 0,08	1.10 ± 0.03	0.56 ± 0.02	0.55 ± 0.02	0.29 ± 0.03	1.31 ± 0.07	2.41 ± 0.12
16	3.97 ± 0.16	1.39 ± 0.10	1.33 ± 0.06	0.68 ± 0.04	0.65 ± 0.05	0.50 ± 0.03	1.48 ± 0.09	2.89 ± 0.08