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Comparison of the Reproductive Characters of Six Species of Scalpellid Barnacles

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The family Scalpellidae is a large family of barnacles containing ca. 200+ nominal species. These barnacles inhabit a wide range of depths, although most species live in the deep sea. These species are dioecious (with large females and dwarf males) or androdioecious (with large hermaphrodites and dwarf males), with one or more dwarf males settling in a specific location (the receptacle) in the larger individuals. We studied the reproductive ecology of six dioecious scalpellid barnacle species in the deep sea, which differ in size and habitat depth. Intraspecific analyses revealed that there was a positive relationship between female size and egg number in all the species, but no significant relationship existed between female size and egg size. No trade-off was detected between the size and number of eggs in a brood. Moreover, there was a positive relationship between female size and the number of dwarf males in three species that possess receptacles that carry more than one male. On the other hand, interspecific analyses suggested that female size was positively related to egg size, egg number, and the number of dwarf males. Considering the large variety of reproductive traits and the many species in this group, further research is needed to elucidate how reproductive traits have evolved in scalpellids.

Keywords: Scalpellidae, Deep-sea barnacle, Egg size and number, Dwarf male, Receptacle

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BACKGROUND

Scalpellidae is a family of pedunculate barnacles that inhabit a wide range of water depths, although most species live in deep seas (Chan et al. 2009; Shalaeva 2014). Most scalpellids are known to have dwarf males attached to much larger hermaphroditic or female individuals, although in a few species, dwarf males have not been identified (Yusa et al. 2012). Among species, the size of females or hermaphrodites varies by more than a factor of 10, and both the number of dwarf males carried and the structure of the site where they are attached (the receptacle) can also vary considerably (Lin et al. 2015; Dreyer et al. 2018c). The monophyly of Scalpellidae is now well established (Chan et al. 2021); thus, how their various reproductive traits have evolved within the group is an interesting question. The reproductive ecology of these species has fascinated many scientists since Darwin (1851). For example, Ozaki et al. (2008) examined the detailed reproductive ecology of *Scalpellum stearnsii* and reported a positive correlation between the weight of females and their egg mass. Lin et al. (2015) and Dreyer et al. (2018c) examined the relationships between microhabitats and the number and types of dwarf males in many species of Scalpellomorpha, whereas Buhl-Mortensen and Høeg (2006 2013) studied in detail the reproductive traits of five selected species, with habitats ranging from shallow to deep seas. Nevertheless, since most scalpellids live in deep seas, samples for ecological studies are difficult to obtain. Accordingly, there remains very limited information on how reproductive traits have evolved within this taxon.

All scalpellids have lecithotrophic larvae (Barnes 1989; Buhl-Mortensen and Høeg 2006). This implies that egg size is an essential component of the reproductive strategy of the parents, as it directly affects fitness through effects on the size and survival of the larvae (Fig. 1). Because females or hermaphrodites produce eggs with limited resources, there is likely a trade-off between offspring size and number (OSN trade-off) (Begon and Parker 1986; Roff 1992). The choice between a few large eggs or many small eggs may depend on factors such as habitat conditions (Duarte and Alcaraz 1989), available resources for the mother, and competition between offspring (Charnov and Skinner 1984). This relationship has not yet been studied in Scalpellidae. One factor that may affect egg size in barnacles is that species from patchily distributed habitats need large nauplii with abundant resources to disperse over long stretches of inhospitable seafloor (Buhl-Mortensen and Høeg 2006; Yorisue et al. 2012). In a comparison of three species, Buhl-Mortensen and Høeg (2006) reported that the sizes of eggs and larvae were positively related to habitat depth. Moreover, some scalpellid species release the larvae as nauplii, whereas other species omit this phase and release them as cyprids, which severely limits their ability to disperse but increases the chance of survival of individual larvae due to a much shorter duration of the pelagic phase.

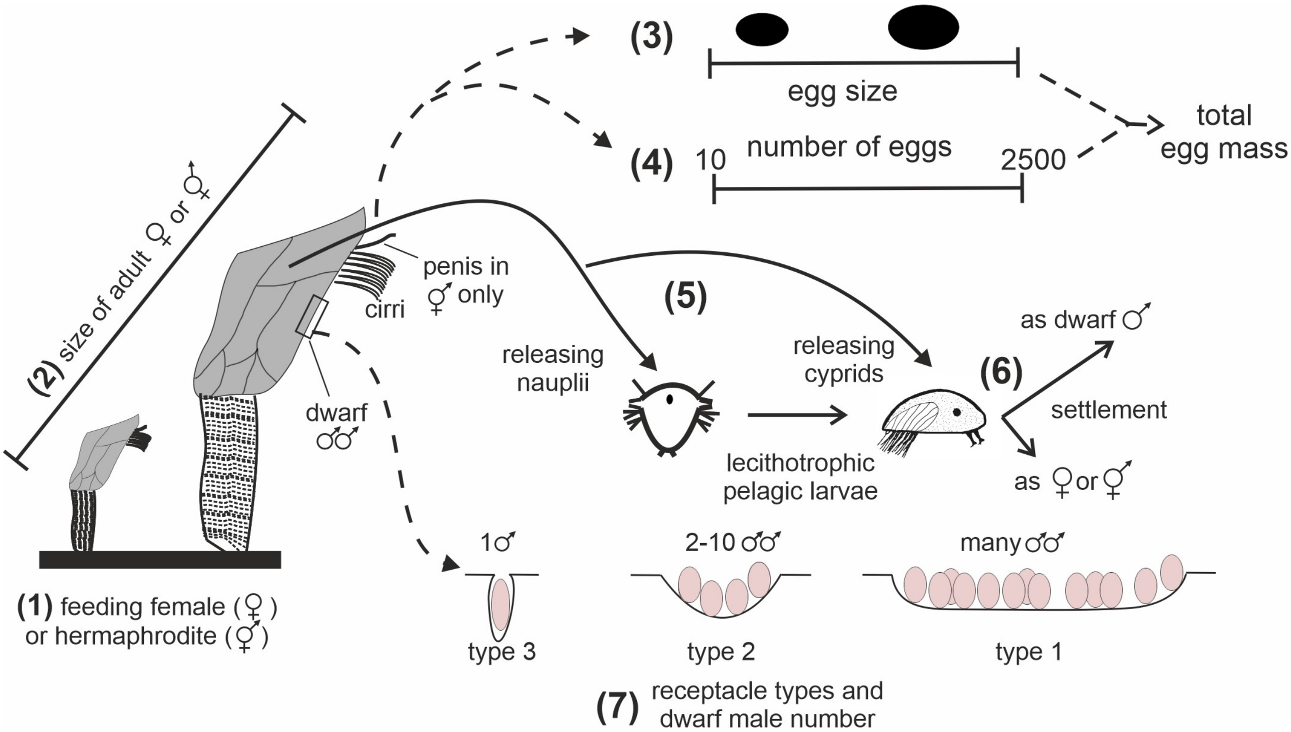

Fig. 1. Reproductive traits of scalpellid barnacles. Populations consist of large, feeding individuals who carry dwarf males in paired receptacles. Important variables between species are as follows (after Buhl-Mortensen and Høeg 2006, 2013; Dreyer et al. 2018c): (1) whether the feeding individual is female (dioecy) or hermaphroditic (androdioecy); (2) the size of the feeding individual; (3) egg size and (4) number of eggs; (5) whether the larvae are released as nauplii or cyprids; (6) the settling of cyprids, which can settle as dwarf males in the receptacles of feeding adults or as females or hermaphrodites on other substrata; and (7) the three types of receptacles and the number of dwarf males they can hold.

Dwarf males of Scalpellidae exhibit a simple oval shape and a specialized, highly reduced structure, consisting mainly of the reproductive organs (Klepal 1987; Buhl-Mortensen and Høeg 2006 2013; Dreyer et al. 2018a b). They reach sexual maturity very soon after settlement and sit protected in relative safety with respect to their large female or hermaphrodite partner (Spremberg et al. 2012; Dreyer et al. 2018b). This implies that dwarf males have an advantage over the hermaphrodites in terms of the male function, because the latter need a much longer time to reach maturity and, during this time, are likely to sustain much higher mortality (Charnov and Downhower 1995). Moreover, they may have a mating advantage over hermaphrodites in the same mating group by being attached directly to their potential mating partner (Urano et al. 2009). Furthermore, unlike some other thoracican species with dwarf males (Yusa et al. 2010), those in scalpellids do not feed. This finding indicates that egg size also directly impacts the size and resources of males, such as the amount of sperm produced and their longevity while attached to their partner.

Larvae that become dwarf males must settle onto a pair of special pocket-like structures called receptacles formed inside the edge of the paired scutal shell plates of their female or hermaphrodite partner (Spremberg et al. 2012; Dreyer et al. 2018c). Owing to the special morphology of the receptacle (Fig. 1), this phenomenon enables females or hermaphrodites to potentially control the number of dwarf males attached (Klepal 1987; Buhl-Mortensen and Høeg 2006 2013; Spremberg et al. 2012; Dreyer et al. 2018c). The size of dwarf males depends directly on egg size and varies somewhat between species, but it is likely the size of the receptacle that principally limits the number of males that can be carried by any individual (Fig. 1). Dreyer et al. (2018c) classified the receptacles in scalpellids into three types. Females or hermaphrodites of species that occur in large, stable microhabitats can grow to a large size and have roomy Type 1 receptacles that can sometimes hold more than 50 males. In contrast, those of species that colonize small, transient microhabitats are smaller, with smaller Type 3 receptacles containing only a few males; in some of these species, the number of males is limited to only two per hermaphrodite or female (one for each of the paired receptacles). Another group of species have intermediate-sized Type 2 receptacles with up to 10–15 males. The number of males carried and female size could be correlated since species with the Type 1 receptacle seem to be large in size, whereas those with the Type 3 are generally small (Buhl-Mortensen and Høeg 2006 2013; Dreyer et al. 2018c).

The aim of this study was to obtain novel information on the reproductive traits of scalpellid barnacles. To achieve this, we examined the reproductive ecology of six species of scalpellids with a relatively large number of samples (n = 16–334). All of these had separate sexes. The reproductive success of females depends both on the number of offspring produced and the survival of individual larvae, which may again depend on their size. We examined parameters likely to affect female reproductive success, such as body size, egg size, egg number (*i.e.*, egg mass size), and the number of males carried (Fig. 1). In general, body size is a crucial factor that affects the resources available for reproduction (Roff 1992; Charnov 1987; Ozaki et al. 2008 for scalpellids). Egg mass size depends on both body size and egg size but may also be affected by the quality and number of dwarf males; unhealthy or insufficient numbers of males may mean that not all eggs produced are successfully fertilized. We accordingly tested five hypotheses, which are not mutually exclusive, regarding reproductive success within each scalpellid species: (1) the body size of the females is positively related to egg number and/or (2) egg size; (3) as a result of 1 and 2, large individuals produce a greater egg mass (*i.e.*, egg number × egg size); (4) there is a trade-off between egg number and size; and (5) body size is positively related to the number of dwarf males carried to ensure both sperm quality and quantity.

MATERIALS AND METHODS

Dataset

Two datasets were used for our analyses: samples collected near Japan and museum collections. The first consisted of Japanese samples collected by YK from 237–3,160 m deep with 3-m beam trawls during 16 research cruises in the period of 2008–2021. These cruises include KS-15-10, KS-17-12, KS-18-8, KS-19-7, KS-19-20, KS-20-15, KS-20-18 and KS-21-14 of R/V Shinsei-maru, KT-11-12, KT-12-18 and KT-12-32 of R/V Tansei-maru, and N275, N295, N307, N319 and N342 of T/V Nagasaki-maru (Appendix 1). Four species with at least 16 female individuals were chosen: 26 individuals of *Teloscalpellum* sp., 38 individuals of *Gymnoscalpellum* sp., 16 individuals of *Amigdoscalpellum* sp., and 20 individuals of *Catherinum* sp. (Fig. 2; Appendix 1). Although identifying them to the species level was not feasible using morphological characters as the scalpellids include many unidentified species, we confirmed that each of the four species comprises a single species using DNA sequences of H3, 18S, and 12S (Hashizoe *et al.*, unpublished data). The collected samples with their substrata were immediately fixed in 99% ethanol, and their reproductive characters were later measured by NH. The second data source was two museum collections. A total of 334 samples of *Ornatoscalpellum gibberum* were collected at the Strait of Magellan in the South Pacific Ocean at a depth of 53 m and were deposited at the National Museum of Natural History, Smithsonian Institute, Washington D.C. A total of 22 *Trianguloscalpellum regium* samples were collected at depths of 2,000–4,800 m and were deposited at the Muséum National d'Histoire Naturelle, Paris. The reproductive characters were measured by JTH.

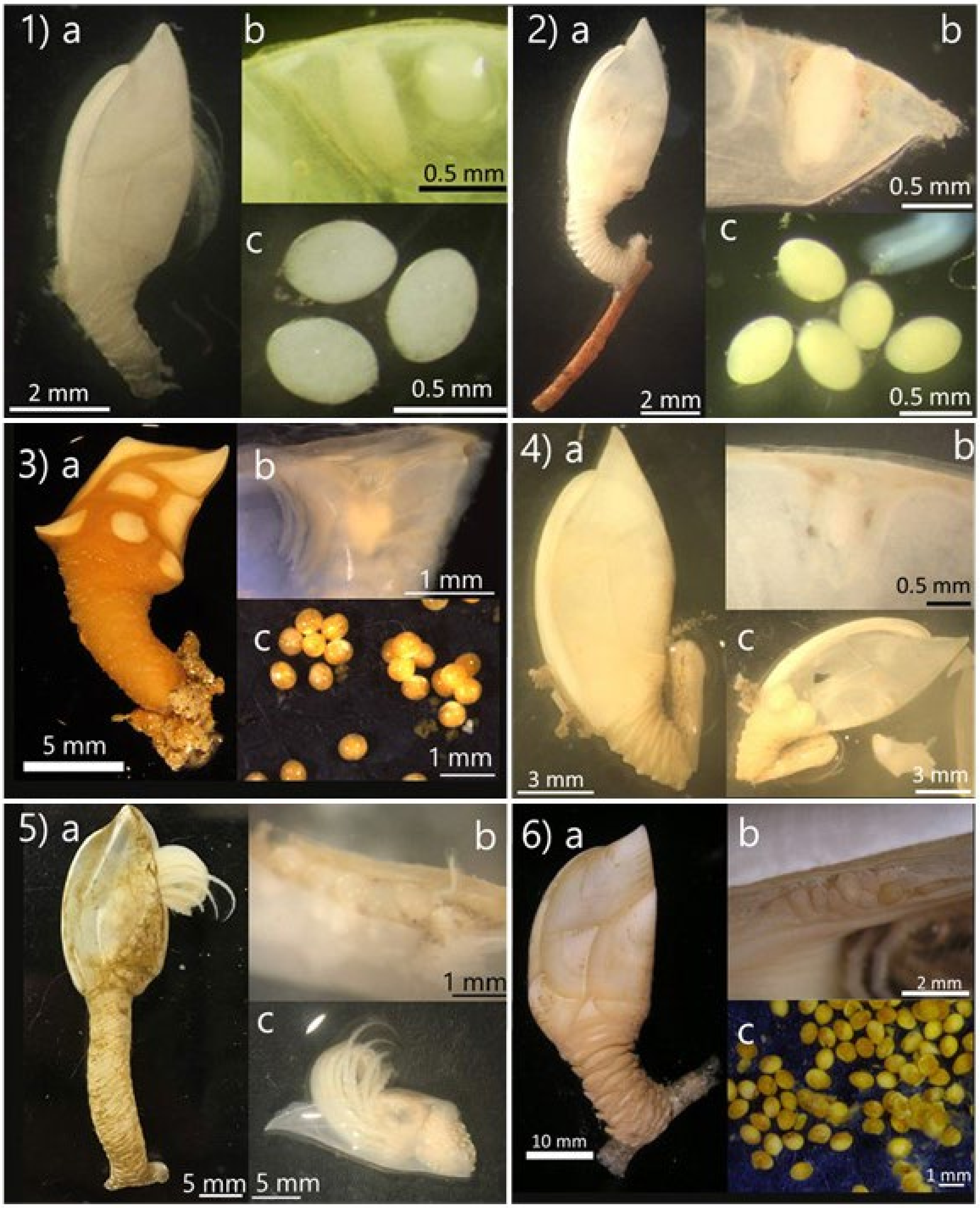

Fig. 2. Six species of scalpellids investigated. 1) *Catherinum* sp.; 2) *Teloscalpellum* sp.; 3) *Ornatoscalpellum gibberum*; 4) *Amigdoscalpellum* sp.; 5) *Gymnoscalpellum* sp.; 6) *Trianguloscalpellum regium*. a, Female; b, dwarf males; c, eggs.

For each female, its capitulum length (and rostrum-carina length; Appendix 1) was recorded as an index of body size. The individual was subsequently dissected, the scutum plate was cut free, and the receptacle type was identified as described by Dreyer et al. (2018c). The total number of dwarf males in both the right and left receptacles was also counted (Dreyer et al. 2018a). Each male was carefully removed from the receptacle with fine tweezers and measured under a stereomicroscope. Settled cyprids attached in or near the receptacles but not yet metamorphosed were also measured and counted as dwarf males. Egg masses were removed if present. The developmental stages of the eggs (egg, early embryo, or nauplius) were recorded, and the major and minor axes of 10 randomly chosen eggs were measured. Finally, the eggs were detached from each other using proteinase K (Wako Pure Chemical Industries, Ltd., Japan), and the number of eggs or embryos was counted. We assumed that the eggs were ellipsoids and calculated their volumes by applying the following formula:

$V = 4/3\pi \times (1/2 \text{ major axis})\times(1/2 \text{ minor axis})^2$. The total egg mass volume was calculated as the egg volume multiplied by the total egg number.

Statistical analyses

All intraspecific analyses were performed by generalized linear models using R version 4.3.0 (R Core Team 2023). We used gamma distribution when the dependent variable was continuous and Poisson distribution when it was count data. Thus, the relationships with egg volume (gamma distribution, log link), egg number (Poisson distribution, log link), egg mass size (gamma distribution, log link), and the number of dwarf males (Poisson distribution, log link) were analysed using capitulum length as the single explanatory variable. In addition, the relationships among capitulum length, egg number (as explanatory variables), and egg size (dependent variable) were analysed (gamma distribution, log link) to examine the existence of a trade-off between the number and size of eggs after controlling for body size.

To investigate whether female body size affects reproductive traits among the six species, the interspecific relationships between female capitulum length and egg size, egg number, or number of dwarf males were studied using Pearson's correlation. For these analyses, the mean values for each species were used.

RESULTS

The capitulum length and reproductive traits for the six species are given in table 1. *Catherinum* sp. had the smallest capitulum length (mean = 5.4 mm), followed by *Teloscalpellum* sp. (5.9 mm), *Ornatoscalpellum gibberum* (8.6 mm), *Amigdoscalpellum* sp. (10.3 mm), *Gymnoscalpellum* sp. (16.7 mm), and *Trianguloscalpellum regium* (36.6 mm). The mean egg number ranged from 21 in *Teloscalpellum* sp. to 820 in *Trianguloscalpellum regium*, but intraspecific variation was also large (Table 1). There was a positive intraspecific relationship between female capitulum length and egg number in all six species ($\chi^2 > 41274.00$, $p < 0.001$) (Fig. 3a; Table 2). The major axis of embryos (egg size) ranged from 459 µm in *Catherinum* sp. to 950 µm in *T. regium* (Table 1). The intraspecific variation was lower than that for egg number, and the capitulum length had no effect on egg size ($\chi^2 < 1.94$, $p > 0.253$). Both *Ornatoscalpellum gibberum* and *Gymnoscalpellum* sp. showed a positive relationship between capitulum length and egg mass size ($\chi^2 = 11.08$, $p < 0.05$) (Fig. 3b; Table 2), but such a relationship was not detected in the other four species ($\chi^2 < 5.29$, $p > 0.099$). The relationships among egg number, egg size, and capitulum length were not significant for any of the six species ($\chi^2 < 5.46$, $p > 0.102$; Table 2).

Table 1. Summary of habitat depth, size, and reproductive traits in six scalpellid species

Species	Depth, m*	Capitulum length, mm**	Receptacle type	Larval release stage
Catherinum sp.	345–1,030 (687.5)	4.1–6.8 (5.4)	Type 3	Nauplius?
Teloscalpellum sp.	1,073	4.8–8.0 (5.9)	Type 3	Nauplius
Ornatoscalpellum gibberum	53	4.7–20.0 (8.6)	Type 2	Cypris
Amigdoscalpellum sp.	436–1,914 (1,175)	7.3–13.8 (10.3)	Type 3	Nauplius?
Gymnoscalpellum sp.	237–3,160 (1,698.5)	11.8–23.5 (16.7)	Type 2	Nauplius?
Trianguloscalpellum regium	2,000–4,800 (3,400)	14.7–50.0 (36.6)	Type 1	Nauplius

Species	Egg number**	Embryo major axis, µm**	Dwarf male number**
Catherinum sp.	6–54 (24)	413–502 (459)	1–2 (1.7)
Teloscalpellum sp.	15–40 (21)	506–650 (572)	1–3 (1.8)
Ornatoscalpellum gibberum	8–2,457 (476)	476–1,124 (630)	1–13 (2.5)
Amigdoscalpellum sp.	32–76 (52)	610–776 (688)	1–4 (1.7)
Gymnoscalpellum sp.	96–784 (281)	500–840 (704)	1–14 (5.4)
Trianguloscalpellum regium	51–1,787 (820)	921–971 (950)	1–56 (10.0)

*Range of the present materials (midpoint of range), **range (mean).

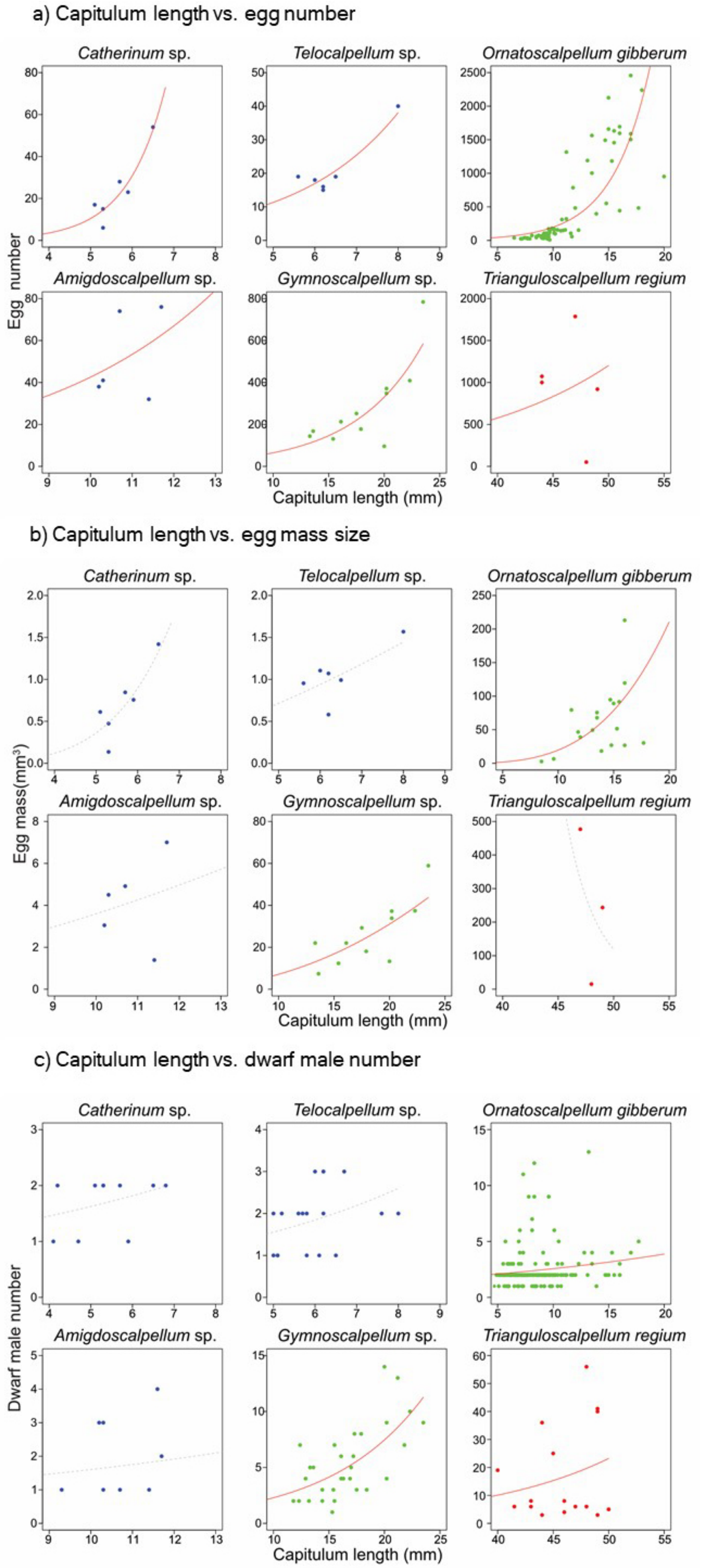

Fig. 3. Results of GLM analyses of the relationships between capitulum length and various reproductive characters in six scalpellid species. Capitulum length vs. a) egg number, b) egg mass

size, and c) dwarf male number. The colours in the plot indicate the following types of the receptacle: red = Type 1, green = Type 2, and blue = Type 3. The regression line is shown in red when significant and in dotted grey when not significant.

Table 2. Results of GLM analyses on the effects of female capitulum length on various reproductive traits

Trait	Species		cofficient(± SE)	*p*
Egg mass size	*Catherinum* sp.	intercept	-0.903(4.01)	0.087
		log(Capitulum)	4.975(2.32)	0.099
	Teloscalpellum sp.	intercept	-2.750(1.66)	0.172
		log(Capitulum)	1.499(0.89)	0.168
	Ornatoscalpellum gibberum	intercept	-4.896(2.35)	0.054
		log(Capitulum)	3.420(0.90)	< 0.05
	Amigdoscalpellum sp.	intercept	-2.708(10.24)	0.809
		log(Capitulum)	1.734(4.30)	0.713
	Gymnoscalpellum sp.	intercept	-2.923(1.90)	0.158
		log(Capitulum)	2.123(0.66)	< 0.05
	Trianguloscalpellum regium	intercept	68.500(150.21)	0.728
		log(Capitulum)	-16.290(38.80)	0.747
Egg number	*Catherinum* sp.	intercept	-7.857(1.70)	< 0.001
		log(Capitulum)	6.309(0.96)	< 0.001
	Teloscalpellum sp.	intercept	-2.090(1.32)	0.113
		log(Capitulum)	2.748(0.70)	< 0.001
	Ornatoscalpellum gibberum	intercept	-4.330(0.06)	< 0.001
		log(Capitulum)	4.138(0.02)	< 0.001
	Amigdoscalpellum sp.	intercept	-1.992(2.69)	0.46
		log(Capitulum)	2.491(1.13)	< 0.05
	Gymnoscalpellum sp.	intercept	-2.865(0.34)	< 0.001
		log(Capitulum)	2.903(0.11)	< 0.001
	Trianguloscalpellum regium	intercept	-5.027(0.51)	< 0.001
		log(Capitulum)	3.093(0.13)	< 0.001
Egg size	*Catherinum* sp.	intercept	-2.574(1.44)	0.149
		log(Capitulum)	-0.543(0.83)	0.551
	Teloscalpellum sp.	intercept	-1.135(1.74)	0.549
		log(Capitulum)	-0.988(0.94)	0.351
	Ornatoscalpellum gibberum	intercept	-2.845(0.19)	< 0.001
		log(Capitulum)	0.048(0.08)	0.557
	Amigdoscalpellum sp.	intercept	1.841(7.13)	0.813
		log(Capitulum)	-1.841(2.99)	0.581
	Gymnoscalpellum sp.	intercept	-1.882(1.41)	0.215
		log(Capitulum)	-0.1411(0.49)	0.779
	Trianguloscalpellum regium	intercept	-5.707(3.11)	0.164
		log(Capitulum)	1.143(0.81)	0.253
Egg size vs. number	*Catherinum* sp.	intercept	-0.314(1.48)	0.845
		log(Egg number)	0.297(0.12)	0.097
		log(Capitulum)	-2.367(1.02)	0.102
	Teloscalpellum sp.	intercept	-1.819(2.05)	0.441
		log(Egg number)	-0.407(0.63)	0.564
		log(Capitulum)	0.0370(1.84)	0.985
	Ornatoscalpellum gibberum	intercept	-2.330(1.30)	0.093
		log(Egg number)	-0.090(0.11)	0.437
		log(Capitulum)	0.076(0.65)	0.909
	Amigdoscalpellum sp.	intercept	3.539(7.59)	0.687
		log(Egg number)	0.492(0.51)	0.437
		log(Capitulum)	-3.361(3.35)	0.421
	Gymnoscalpellum sp.	intercept	-2.045(1.38)	0.175
		log(Egg number)	-0.296(0.20)	0.180
		log(Capitulum)	0.472(0.64)	0.484
	Trianguloscalpellum regium	intercept	2.147(NA)	NA
		log(Egg number)	-0.039(NA)	NA
		log(Capitulum)	0.824(NA)	NA
Dwarf male number	*Catherinum* sp.	intercept	-0.495(2.58)	0.848
		log(Capitulum)	0.613(1.53)	0.688
	Teloscalpellum sp.	intercept	-1.445(2.15)	0.501
		log(Capitulum)	1.154(1.19)	0.334
	Ornatoscalpellum gibberum	intercept	0.049(0.33)	0.882
		log(Capitulum)	0.396(0.16)	< 0.05

	Amigdoscalpellum sp.	intercept	-1.983(3.28)	0.545
		log(Capitulum)	1.069(1.39)	0.443
	Gymnoscalpellum sp.	intercept	-4.104(1.23)	< 0.001
		log(Capitulum)	2.0452(0.43)	< 0.001
	Trianguloscalpellum regium	intercept	-8.607(1.04)	< 0.001
		log(Capitulum)	2.982(0.28)	< 0.001

NA: not applicable.

Catherinum sp. and *Amigdoscalpellum* sp. had the smallest number of dwarf males (mean = 1.7), followed by *Teloscalpellum* sp. (1.8), *O. gibberum* (2.5), *Gymnoscalpellum* sp. (5.4), and *T. regium* (10.0) (Table 1). A positive relationship was detected between female capitulum length and dwarf male number in *O. gibberum* ($\chi^2 = 6.39$, $p < 0.05$), *Gymnoscalpellum* sp. ($\chi^2 = 23.25$, $p < 0.001$), and *T. regium* ($\chi^2 = 168.52$, $p < 0.001$) (Fig. 3c; Table 2). No such relationship was observed in the other three species ($\chi^2 < 6.39$, $p > 0.334$).

Interspecific comparisons among the six species revealed that female capitulum length had positive effects on the mean egg number ($N = 6$, $r = 0.858$, $p < 0.05$), egg size ($r = 0.942$, $p < 0.01$), and number of dwarf males ($r = 0.982$, $p < 0.001$). There was a positive correlation between the midpoint of depth of collection sites and mean female capitulum length ($N = 6$, $r = 0.928$, $p < 0.01$), and between depth and egg size ($r = 0.850$, $p < 0.05$).

DISCUSSION

Intraspecific relationships

A positive relationship was found between capitulum length and egg number in all six scalpellid species (Fig. 3a). Such a relationship has also been reported in other scalpellids, *Scalpellum scalpellum* (Buhl-Mortensen and Høeg 2006) *and S. stearnsii* (Ozaki et al. 2008), which suggests that this relationship is common in the family. As larger females have more resources and brood space for producing and rearing eggs, they likely increase the number of eggs to maximize their fitness, which results in a positive relationship between female size and egg number.

On the other hand, there was no intraspecific relationship between female capitulum length and egg size in any of the six species. The lack of such a relationship suggests that there is an optimal egg size for each species regardless of the mother’s size. Scalpellids have lecithotrophic larvae (Buhl-Mortensen and Høeg 2006), and the larvae must rely on the resources provided through the egg for survival during the larval period, settlement, and metamorphosis. Moreover, for larvae to settle as nonfeeding dwarf males, the resources provided through the egg must sustain sperm production. Therefore, scalpellids likely cannot reduce their egg size below a threshold (Winkler and Wallin 1987). The theory of optimal egg size (Smith and Fretwell 1974) also predicts that a mother should produce offspring of a certain size regardless of her body size. Although a trade-off between egg size and number is common in many organisms (Smith and Fretwell 1974; Stearns 1989), no such relationship was found among the scalpellids examined here. The lack of such a trade-off may reflect that scalpellids have an optimal egg size for each species, as explained, and hence, intraspecific variation in egg size is low.

Egg mass size, used as an index of female reproductive output, was related to the size of females only in *O. gibberum* and *Gymnoscalpellum* sp. This may rather reflect, however, their larger sample sizes (n = 18 and 11, respectively; Appendix 1) than the other species (n ≤ 6) where significant relationships might also be detected by examining more specimens. In addition, the lifetime female reproductive output is a function of the number of broods, as well as egg mass size (Buhl-Mortensen and Høeg 2006). The number of broods is notoriously difficult to measure, and a careful rearing experiment simulating natural conditions is needed to quantify this life history trait.

A positive relationship was found between female size and the number of dwarf males carried in *O. gibberum*, *Gymnoscalpellum* sp., and *T. regium*. Both *O. gibberum* and *Gymnoscalpellum* sp. have the middle-sized Type 2 receptacles (Dreyer et al. 2018c). *Trianguloscalpellum regium* was the only species with the large Type 1 receptacles in this study. In contrast, no relationship between female size and male number was detected in the species with the small Type 3 receptacles. This Type 3 receptacle is a deep, narrow pocket that can normally accommodate only a single male, thus limiting the male number per female to two, irrespective of body size. In contrast, females with Type 1 or Type 2 receptacles can harbour many males. It is unknown whether many males are needed to fertilize the many eggs produced by large females; males may simply accumulate on larger and older females, which results in a positive relationship between size and male number. Alternatively, male larvae may prefer to settle on large females with many eggs rather than smaller ones with few eggs to maximize their fitness.

Interspecific relationships

Our analyses revealed positive effects of female size on egg number, egg size, and dwarf male number among the six species. The interspecific relationship between female size and egg number reflects that larger females tend to have more resources for egg production and more brood space, as already discussed with respect to intraspecific variation. A positive relationship between female size and egg size was found in the interspecific comparisons but not in the intraspecific comparisons. This interspecific relationship may be associated with the positive correlation between depth and female capitulum length and between depth and egg size. Buhl-Mortensen and Høeg (2006, 2013) suggested that the size of eggs was related to habitat depth and reported that species from patchily distributed habitats need large nauplii to disperse over long distances. In this study, cyprids were found in the brood chamber only in *Ornatoscalpellum gibberum*. These findings suggest that the other species likely release their larvae as nauplii, although the degree of extended brooding did not seem to affect egg size (Table 1).

The observed interspecific relationship between female size and male number in the six scalpellid species was consistent with the findings of Dreyer et al. (2018c), who reported that species with large females have more males than those with smaller females. Three species with relatively small females (*Catherinum* sp., *Teloscalpellum* sp., and *Amigdoscalpellum* sp.) had Type 3 receptacles and an average of less than two males in each female (Table 1). *Trianguloscalpellum regium* had the largest females with Type 1 receptacles, which can harbour many males. Buhl-Mortensen and Høeg (2013) also found that the number and position of dwarf males is related to the morphology of the receptacles, and discussed that these traits were adapted to secure the fertilization for females or hermaphrodites.

However, our interspecific analyses should be considered preliminary. Although reproductive data on the scalpellids have been accumulated (Barnes 1989; Buhl-Mortensen and Høeg 2006, 2013; Dreyer et al. 2018c), more data for rare species are needed to derive any concrete conclusions. The expected lack of independence of observations across different species should also be taken into account with a robust phylogenetic framework and statistical methods that incorporate relatedness (*e.g.*, Yusa et al. 2012; Lin et al. 2015 on barnacles).

CONCLUSIONS

This study provides novel data on the reproductive traits of six scalpellid species, such as positive intraspecific relationships between capitulum length and the number of eggs or dwarf males. Such relationships have rarely been demonstrated in scalpellids because of the difficulty in obtaining large numbers of samples from deep seas. Our preliminary interspecific analyses suggest that female size increases with depth and, in turn, affects the number and size of eggs and the number of males. The species-rich Scalpellidae is a very promising group for analysing the evolution of reproductive systems. Considering the large variety of habitats and large number of species of scalpellid barnacles, further study is needed to elucidate their reproductive ecology. Such studies will be assisted by the emerging understanding of the phylogeny of the taxon, enabling phylogenetic signals to be separated from other factors (Chan et al. 2021).

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Supplementary materials

Appendix 1. Raw data of six scalpellid species. (download)