



Length–weight relationships to quantify biomass for motile coral reef cryptofauna

Kennedy Wolfe¹ · Amelia Desbiens^{1,2} · Jessica Stella³ · Peter J. Mumby^{1,4}

Received: 30 April 2020 / Accepted: 10 August 2020 / Published online: 20 August 2020
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

Abstract Length–weight relationships (LWRs) are a fundamental tool for the non-intrusive determination of biomass, a unit of measure that facilitates the quantification of ecosystem and fisheries productivity. LWRs have been defined and broadly applied for many marine species across a range of ecosystems, especially regarding fishes. However, LWRs are yet to be determined for the majority of marine taxa, particularly for small cryptic organisms that are difficult to census and poorly described. On coral reefs, the motile cryptofauna represent the greatest density and diversity of metazoan taxa that likely support critical steps in trophic pathways, but little empirical data exist beyond biodiversity assessments. We evaluated LWRs for 42 groups of motile cryptofauna across four microhabitats (live *Acropora*, live *Pocillopora*, dead branching coral and coral rubble) in Palau, Western Micronesia. We employed a robust methodology to determine LWRs by comparing the suitability of a series of linear, quadratic, polynomial

and power models. Using the best-fit equations for each group, we provide the first documented LWRs for motile cryptofauna, namely at the level of family. LWRs were well fit ($R^2 > 0.90$) for 45% of the groups and reasonable ($R^2 > 0.70$) for 76%. The presence, size and weight of cryptofauna varied among microhabitats with the size distribution of 13 groups significantly influenced by habitat type. Establishment of these LWRs provides critical baseline information regarding an overlooked group on coral reefs, making population data on the cryptofauna more accessible to support future research aiming to characterise the roles of these taxa in ecosystem functioning and trophodynamics.

Keywords Biometrics · Coral reefs · Invertebrate · Microhabitat · Rubble

Introduction

Ecology is founded on patterns in the density and abundance of species within an ecosystem. For conspicuous organisms, density data are generally easily obtained through non-intrusive in situ survey methods including belt transects and videography. Abundance, on the other hand, is often quantified in terms of biomass, an important indicator for assessing the condition or productivity of an ecosystem (Griffiths 1986; Warwick and Clarke 1994; Odum 2013). However, quantification of biomass has historically depended on the harvest and sacrifice of a sufficient number of individuals from a population. To abate this issue, determination of biometrics, such as length–weight relationships (LWRs), has gained traction in marine ecology.

Topic Editor Morgan S. Pratchett

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00338-020-01993-9>) contains supplementary material, which is available to authorised users.

✉ Kennedy Wolfe
k.wolfe@uq.edu.au

¹ Marine Spatial Ecology Lab, School of Biological Sciences and ARC Centre of Excellence for Coral Reef Studies, University of Queensland, St Lucia, QLD 4072, Australia

² The Australian Rivers Institute, Griffith University, Nathan, QLD 4111, Australia

³ Great Barrier Reef Marine Park Authority, Townsville, QLD 4810, Australia

⁴ Palau International Coral Reef Center, PO Box 7096, Koror 96940, Republic of Palau

LWRs improve our understandings of marine ecosystems from the level of individuals through to community dynamics (Duplisea et al. 2002; Jennings et al. 2002, 2007; Robinson et al. 2010) and ecosystem productivity (Brey 1990; Edgar 1990). Estimation of biomass using LWRs is essential for upscaling ecological surveys with many applications including in fish stock assessments and evaluation of food web dynamics (Duplisea et al. 2002; Jennings et al. 2002; Bascompte et al. 2005; Robinson et al. 2010). It is therefore not surprising that determination of LWRs in marine ecosystems has largely focused on fishes (Bohnsack and Harper 1988; St John et al. 1990; Letourneur et al. 1998; Kulbicki et al. 2005; Balart et al. 2006; Froese 2006). Online resources, such as FishBase, are a repository for LWRs for thousands of fishes of the world (Froese and Pauly 2018), making them easily accessible and therefore widely employed.

Despite their relatively small contribution to total coral reef biodiversity (Reaka-Kudla 1997), ecological research and monitoring have largely focused on reef fishes and corals (Bellwood and Hughes 2001; Przeslawski et al. 2008; Fisher et al. 2015; Bellwood et al. 2017), as they are easy to census and their taxonomy is relatively well known. However, metazoan biomass of most ecosystems, including coral reefs, is dominated by cryptic invertebrate fauna (Wilson 1992; Reaka-Kudla 1997). For coral reef invertebrates, establishment of LWRs has largely been reserved for conspicuous fauna with commercial or ecological importance, including aspidochirotid sea cucumbers (Conand 1993; Pitt and Duy 2004; Natan et al. 2015; Lee et al. 2018), diadematid sea urchins (Rahman et al. 2012), penaeid prawns (Fontaine and Neal 1971; Penn 1980), spiny lobsters (Ebert and Ford 1986; Wade et al. 1999; Vaitheeswaran et al. 2012; Aisyah and Triharyuni 2017) and trochid gastropods (Klumpp and Pulfrich 1989; Saleky et al. 2016). Owing to their large size, determination of biometrics for these groups can be conveniently and directly measured with little training. Determination of biometrics for motile cryptofauna—cryptobenthic organisms that typically take refuge inside the complexities of the reef matrix and dominate total reef biomass and diversity (Peyrot-Clausade 1979; Hutchings 1983; Plaisance et al. 2011; Takada et al. 2012; Carvalho et al. 2019)—is more challenging (Brock 1982; Alzate et al. 2014).

Owing to their interstitial tendencies, the cryptofauna are difficult to observe and are therefore poorly described and monitored (Hutchings 1983; Reaka-Kudla 1997; Glynn 2013). Given that the majority of motile cryptofauna are closely associated with their microhabitat, surveying these taxa usually involves sampling the entire microhabitat (e.g. a whole coral colony) (e.g. Alzate et al. 2014; Fraser et al. 2020), which is laborious, time-consuming and often

destructive. Thus, data on the biometrics of motile coral reef cryptofauna are scarce (but see Opitz 1993; Balart et al. 2006), though some effort has been made for small mobile invertebrates in other marine ecosystems (e.g. Taylor 1998; Robinson et al. 2010) including in the zooplankton (Cohen and Lough 1981; Uye 1982; Heron et al. 1988; Watkins et al. 2011).

The cryptofauna are a foundation group in coral reef trophic pathways, as outlined in great detail for cryptobenthic fishes (Brandl et al. 2018, 2019). Biodiversity of the motile cryptofauna is largely determined by microhabitat type and reef degradation profiles (Hutchings 1983; Reaka-Kudla 1997; Enochs et al. 2011), which consequently influences invertebrate–invertevore interactions from the bottom-up (Rogers et al. 2014; Kramer et al. 2016; Rogers et al. 2018a). Dead coral and coral rubble often host the most abundant and diverse populations of metazoan fauna on coral reefs (Takada et al. 2007; Enochs 2012; Enochs and Manzello 2012). In contrast, cryptic organisms that occupy live coral tend to be specialised associates, including decapods of the Tetraliidae and Trapeziidae (Stella et al. 2011). Yet, little empirical data exist on the taxonomy, population structure and characteristics of motile cryptofauna beyond biodiversity assessments. Moving beyond such assessments through quantification of biomass and rates of reproduction, growth and population turnover is critical to determining the roles of motile cryptofauna in ecosystem productivity and reef-scale trophodynamics (Rogers et al. 2018b).

As exists for corals (e.g. Coral Trait Database: Madin et al. 2016) and fishes (e.g. FishBase: Froese and Pauly 2018), we provide baseline information that can be used to extrapolate size and biomass for motile cryptofauna in future endeavours. Availability of these morphometric relationships will relieve the requirement of destructive and sacrificial sampling methods and encourage the application of multi-model biometric analyses in coral reef and marine ecology. These data may also enable estimations of biomass to be conducted via fine-scale visual underwater surveys for more conspicuous cryptofauna taxa (i.e. live coral specialists), rather than current methods requiring destructive microhabitat sampling.

Methods

Specimen collection and processing

Samples from four microhabitat types (live *Acropora*, live *Pocillopora*, dead branching coral and coral rubble; Fig. S1) were collected from the east coast of Palau, Western Micronesia (Dec 2014–Feb 2015) to quantify the motile cryptofauna population. Specimens were sampled

from these four microhabitats to ensure the best representation of individuals across a range of cryptobenthic taxa encompassing habitat specialists and generalists. Replicate substrate samples ($n = 23\text{--}24$) and their resident cryptofauna were collected at 5–7 m depth across various sites. For live (*Acropora* and *Pocillopora*) and dead (*Acropora*) coral microhabitats, cryptofauna were collected by covering the entire coral colony with a plastic bag to prevent mobile organisms from escaping, and the entire intact colony was carefully chiselled free of the substrate and sealed in the bag underwater. Coral rubble samples were collected by inserting plastic mesh trays ($22 \times 18 \times 5.8$ cm) filled with defaunated rubble in place of a natural rubble patch. All rubble pieces were derived from dead branching coral fragments. The rubble containers were left in the field for ~ 7 d to allow inhabitants ample opportunity to resettle. Upon retrieval, trays were lifted from their depression and placed into plastic bags, as the above. All communities were transferred into individual buckets of seawater and transported back to the laboratory within 2 h for processing.

To extract cryptofaunal specimens, each microhabitat sample was searched extensively for conspicuous fauna that could be easily removed using blunt probes, forceps and plastic spoons and were placed into petri dishes for identification. The microhabitats were then washed with pressurised seawater over a tray to dislodge any fauna clinging to the surface. This was done several times with close inspection between washes. Water from the respective collection bags and wash trays was then poured through mesh net (1×1 mm) and all fauna retrieved for identification under a dissecting microscope (this method excluded individuals < 1 mm). Each organism was identified to the highest taxonomic resolution possible (namely to family) and measured to the nearest 0.1 mm. Standard measurements were used: carapace width for crab-like crustaceans or length for shrimp-like crustaceans, shell length for molluscs (widest distance), diameter for echinoderms with radial symmetry and length for all types of worms. Each individual was then placed in a dry petri dish to be weighed to the nearest mg using an analytical balance (AND GR-120). Residual water was blotted off using fine tissue paper under the microscope before weight was recorded. All shelled specimens remained shelled for length and weight measurements. All faunae were released with their respective microhabitat at their original site of collection.

Length–weight relationships

Length (mm) and weight (g) data were used to determine LWRs for 42 taxonomic groups to make population and biometric data more accessible for this overlooked group.

To calculate LWRs, data were combined across all four microhabitat types for each group of cryptofauna. LWRs were only produced for groups represented by ≥ 17 individuals in the dataset. Groups represented by < 17 individuals were excluded from all analyses. Consequently, total densities of cryptofauna were not determined.

Statistical analyses

LWRs have typically been determined for single species or among morphometrically similar groups (i.e. fishes) using the power model equation: $W = aL^b$ (Kulbicki et al. 2005; Froese 2006; Saleky et al. 2016; Lee et al. 2018), including for those stored on FishBase (Froese and Pauly 2018). Determination of LWRs from multiple models is particularly important when addressing taxa across a diversity of sizes and morphologies, as shown previously for invertebrates in terrestrial systems (Gowing and Recher 1984; Ganihar 1997). Thus, LWRs were assessed here using linear, quadratic, polynomial and power functions to determine the best possible fit of data for each group. Model selection was determined using second-order Akaike Information Criterion (AICc) values in the *MuMin* package of R (Sakamoto et al. 1986; Bartoń 2018). Each best-fit LWR was then examined graphically to explore potential model over-fitting. Where necessary, alternate models were assessed and selected based on predicted R^2 values, which are an effective selection criterion that consider model predictive power and, when compared to regular R^2 values, provide a strong indication of model over-fitting (Allan 1974; Cawley and Talbot 2010). Predicted R^2 values were calculated using the Prediction of Sum-of-Squares (*PRESS*) statistic function in the *qpcR* package (Spiess 2018). Alternate model selection was completed for 14 groups. For power models, data were log transformed before determining LWRs, but back-transformations were conducted before producing the final equations. The equation of each best-fit model is presented in Table 2 along with the respective model type and strength of relationship (R^2).

Differences in cryptofauna size among the four microhabitat types were examined using one-way analysis of variance (ANOVA) in the *stats* package (R Core Team 2019). Separate ANOVAs were conducted for each cryptofauna group. Two families found in just one microhabitat (Cancellaridae in rubble, Epiplatidae in dead coral) were excluded from this analysis, as were data for single specimens within a microhabitat. As required for ANOVA, normality and homogeneity of variance were explored visually using residual and quantile–quantile plots in the *ggfortify* package (Tang et al. 2016). For all models, post hoc Tukey’s pairwise comparisons were performed using the *emmeans* package when significant differences (p

≤ 0.05) were detected (Lenth 2019). All model development and analyses were conducted in R 3.6.3 (R Core Team 2019).

Results

Length–weight relationships

A total of 4581 individuals were identified and measured, but there were insufficient data for 624 individuals (i.e. groups with $n < 17$). LWRs were produced for 42 groups of motile coral reef cryptofauna using empirical length and weight measurements for 3957 individuals (Tables 1, 2; Fig. S2). Sample size of each group ranged from 574 individuals for the Amphipoda to 17 individuals for the Epialtidae and Limidae (mean \pm SE: 94.2 ± 18.3 individuals) (Table 1). Model selection resulted in a range of best-fit linear (19%), quadratic (55%), polynomial (24%) and power (2%) relationships across all groups (Table 2; Fig. 1, S1). There were no similarities evident in the best-fit model type based on taxonomy (Table 2; Fig. S2).

LWRs were well fit ($R^2 > 0.90$) for 45% of the groups assessed (Fig. 2), while 76% of groups had an R^2 above 0.70 (Table 2). The strongest relationships ($R^2 \geq 0.99$) were determined for hippolytid decapods and molluscs of the Conidae, Dialidae, Fasciolariidae and Phasianellidae (Table 2; Fig. 2). The best-fit LWR for the worms (Polychaeta) was found for the Nereididae ($R^2 = 0.95$) (Table 2; Fig. 2). Some groups exhibited poorly fit LWRs regardless of model type, especially regarding the Caprellidae ($R^2 = 0.001$) and Tanaidacea ($R^2 = 0.19$) (Table 2), owing to their consistently low and variable weights, respectively (Table 1; Fig. S2). The Caprellidae exhibited the minimum weight range (0.001–0.002 g) despite a range in length of 4.1–9.5 mm (Table 1; Fig. S2). Most poorly fit LWRs ($R^2 < 0.55$) (Table 2; Fig. S2) existed for groups with the lowest weight ranges (≤ 0.01 g) (Table 1), including the Amphinomidae, Caprellidae, Isopoda, Joeropsididae and Tanaidacea. Notably, molluscs with low weights (< 0.02 g) (e.g. Cancellaridae, Pyramidellidae, Terebridae; Table 1) exhibited reliable LWRs ($R^2 > 0.80$) (Table 2).

Microhabitat drivers

Motile cryptofauna were more abundant in dead coral and coral rubble compared to live coral (Table 3, S1). Live *Acropora* hosted the lowest numbers of cryptofauna by over an order of magnitude compared to dead coral and rubble (Table 3, S1). Conversely, live coral hosted a greater mean size (length) of cryptofauna by around two-fold compared to dead coral and rubble (Table 3). Live *Acropora* and *Pocillopora* also hosted a greater mean

weight of cryptofauna by three- and sixfold, respectively, compared to dead coral and rubble (Table 3).

Two of the 42 groups of motile cryptofauna for which LWRs were calculated were found in just one habitat: Cancellaridae in rubble and Epialtidae in dead coral (Table S1). Seventeen groups were not found in live coral with an additional 12 groups represented by just one or two individuals in live coral (Table S1). Conversely, the Tetraliidae were predominately found in live *Acropora* with just one individual found in dead coral (Table S1).

Size distributions of 13 groups of motile cryptofauna were significantly influenced by microhabitat (Table S2; Fig. 3, S3). Decapods of the Alpheidae and Trapeziidae were largest in live coral, as were Limidae bivalves (Fig. 3, S3). Bivalves of the Mytilidae were largest in dead coral compared to rubble (Fig. 3, S3), yet one large individual was found in live *Acropora* (Table S1). Members of the Palaemonidae and Turbinidae also exhibited significantly greater sizes in live coral (*Acropora* or *Pocillopora*) (Fig. 3, S3). Two groups of ophiuroids (Ophiactidae and Ophiomyxidae) were largest in live *Pocillopora* (Fig. 3). Diogenidae were largest in both live *Pocillopora* and coral rubble (Fig. 3). The Caprellidae and Xanthidae were significantly larger in rubble, while the Columbelloidae were largest in dead coral despite exhibiting a broad size range in rubble (Table S2; Fig. 3). No Caprellidae were found in live coral, and just one individual from the Columbelloidae was found in live coral (*Pocillopora*) (Table S1). Trapeziid decapods were not found in rubble (Table S1).

Discussion

Length–weight equations are provided for 42 groups of motile coral reef cryptofauna to support future research aiming to evaluate this level of biodiversity and upscale consideration of their roles in ecosystem functioning and productivity. LWRs are yet to be empirically determined for such a diversity of coral reef phyla nor through comparison of four model types, as done here. Calculated LWRs were generally well fit (76% with $R^2 > 0.70$), although some were particularly unreliable (e.g. Caprellidae: $R^2 = 0.001$). Groups with the lowest weights (≤ 0.01 g) tended to exhibit the weakest LWRs attributing to the difficulties in attaining fine-scale length and weight data for motile microfauna. Converse to that documented for terrestrial invertebrates (Ganihar 1997), there were no similarities evident in best-fit model type based on taxonomy, highlighting the importance of considering multiple model types in the determination of LWRs across morphologically diverse taxa.

LWRs were fit across all four microhabitats (live *Acropora*, live *Pocillopora*, dead coral and rubble),

Table 1 Minimum, mean (\pm SE) and maximum length (mm) and weight (g) of 42 groups of motile cryptofauna, including total sample size (n) used to calculate length–weight relationships

Phylum	Class	Order	Family	n	Length (mm)			Weight (g)			
					Min	Mean \pm SE	Max	Min	Mean \pm SE	Max	
Annelida	Polychaeta	Amphinomida	Amphinomidae	28	2.2	6.9 \pm 0.8	16.6	0.001	0.009 \pm 0.002	0.049	
		Phyllodocida	Nereididae	22	3.1	10.3 \pm 2.0	38.6	0.001	0.006 \pm 0.002	0.050	
			Polychaeta*	195	0.1	7.9 \pm 0.4	40.6	0.001	0.005 \pm 0.001	0.183	
Mollusca	Gastropoda	Heterobranchia	Bullidae	48	0.8	2.1 \pm 0.2	6.1	0.001	0.008 \pm 0.002	0.088	
				Pyramidellidae	25	1.1	3.0 \pm 0.2	4.4	0.001	0.005 \pm 0.001	0.019
				Vetigastropoda	Haliotidae	57	1.3	4.3 \pm 0.3	8.4	0.002	0.046 \pm 0.006
				Phasianellidae	25	1.3	3.4 \pm 0.4	9.9	0.001	0.024 \pm 0.011	0.226
		Caenogastropoda	Dialidae	33	1.2	2.4 \pm 0.2	9.1	0.001	0.008 \pm 0.005	0.156	
			Potamididae	275	0.7	3.4 \pm 0.2	34	0.001	0.036 \pm 0.023	6.105	
		Neogastropoda	Buccinidae	42	1.1	3.6 \pm 0.4	11.5	0.001	0.056 \pm 0.026	0.816	
			Cancellaridae	31	1.9	2.9 \pm 0.2	5.8	0.002	0.005 \pm 0.001	0.019	
			Columbellidae	35	2.1	8.0 \pm 0.6	12	0.003	0.237 \pm 0.035	0.596	
			Conidae	19	3.7	8.4 \pm 0.9	18.8	0.015	0.267 \pm 0.087	1.646	
			Costellariidae	48	1.1	3.0 \pm 0.2	7.7	0.001	0.009 \pm 0.003	0.104	
			Fasciolaridae	118	1.1	4.4 \pm 0.2	20.8	0.001	0.034 \pm 0.009	1.014	
			Mitridae	19	0.4	3.1 \pm 0.4	6.1	0.001	0.011 \pm 0.003	0.050	
			Muricidae	83	2.3	10.6 \pm 0.6	22.4	0.004	0.476 \pm 0.062	3.410	
			Terebridae	30	1.1	3.6 \pm 0.2	6.4	0.001	0.006 \pm 0.001	0.016	
			Trochida	Turbinidae	50	0.2	2.7 \pm 0.6	22.2	0.001	0.143 \pm 0.078	2.996
			Bivalvia	Limida	Limidae	17	2.6	7.3 \pm 0.9	13.1	0.004	0.098 \pm 0.033
Mytilida	Mytilidae			24	1.6	6.9 \pm 1.0	22.3	0.003	0.129 \pm 0.053	1.085	
Arthropoda	Malacostraca	Amphipoda	Amphipoda*	574	1.1	3.6 \pm 0.1	8.7	0.001	0.003 \pm 0.0001	0.020	
				Caprellidae	23	4.1	6.1 \pm 0.4	9.5	0.001	0.001 \pm 0.0001	0.002
				Isopoda	Anthuridae	20	2.2	5.4 \pm 0.5	10.4	0.001	0.003 \pm 0.0004
				Isopoda*	139	0.8	3.0 \pm 0.1	5.6	0.000	0.004 \pm 0.0002	0.012
				Joeropsididae	29	0.2	2.6 \pm 0.1	7.2	0.001	0.002 \pm 0.0002	0.005
		Tanaidacea	Tanaidacea*	132	1.1	3.1 \pm 0.1	6.6	0.001	0.007 \pm 0.001	0.048	
		Decapoda	Alpheidae	166	2.3	10.1 \pm 0.5	30.1	0.001	0.113 \pm 0.017	0.904	
			Diogenidae	111	2.4	14.7 \pm 0.7	41.6	0.019	1.183 \pm 0.170	12.03	
			Epialtidae	17	1.6	3.4 \pm 0.5	7.3	0.004	0.102 \pm 0.037	0.440	
			Galatheididae	435	0.4	2.1 \pm 0.04	4.1	0.001	0.019 \pm 0.001	0.093	
			Hippolytidae	103	1.8	6.6 \pm 0.3	27	0.001	0.011 \pm 0.004	0.369	
			Majidae	22	1	2.9 \pm 0.3	6.3	0.002	0.054 \pm 0.016	0.247	
			Paguridae	39	1.1	4.8 \pm 0.4	12.2	0.003	0.049 \pm 0.012	0.292	
			Palaemonidae	196	2.8	9.3 \pm 0.2	16.8	0.001	0.022 \pm 0.001	0.104	
			Pilumnidae	19	1.7	2.7 \pm 0.3	5.2	0.001	0.019 \pm 0.007	0.110	
			Portunidae	62	1.8	8.3 \pm 0.6	20	0.001	0.229 \pm 0.033	1.014	
		Tetraliidae	54	2.1	6.6 \pm 0.3	11.1	0.004	0.225 \pm 0.022	0.604		
Trapeziidae	181	1.7	6.5 \pm 0.2	14.2	0.003	0.313 \pm 0.029	1.565				
Xanthidae	329	0.4	4.7 \pm 0.2	14	0.001	0.132 \pm 0.013	1.420				
Echinodermata	Ophiuroidea	Amphilepidida	Ophiactidae	45	0.1	1.4 \pm 0.1	5.5	0.001	0.011 \pm 0.004	0.174	
		Ophiacanthida	Ophiomyxidae	37	0.8	3.1 \pm 0.4	7.8	0.001	0.095 \pm 0.025	0.563	

Asterisk indicates higher levels of taxonomy

Table 2 Length–weight relationships for 42 groups of motile cryptofauna, including fit type and R^2 value

Phylum	Class	Order	Family	Fit type	R^2	Equation	
Annelida	Polychaeta	Amphinomida	Amphinomidae	Linear	0.364	$W = -0.0010 + 0.0014 * L$	
			Nereididae	Quadratic	0.949	$W = 0.0013 - 0.00004 * L + 0.00003 * L^2$	
	Gastropoda	Phyllodocida	Polychaeta*	Polynomial	0.773	$W = -0.00048 + 0.00025 * L - 0.0002 * L^2 + 0.000006 * L^3$	
			Bullidae	Quadratic	0.796	$W = 0.0074 - 0.0068 * L + 0.0026 * L^2$	
		Vetigastropoda	Pyramidelidae	Polynomial	0.840	$W = 0.0010 + 0.0007 * L - 0.0008 * L^2 + 0.0003 * L^3$	
			Haliotidae	Quadratic	0.885	$W = 0.0054 - 0.0065 * L + 0.0031 * L^2$	
		Caenogastropoda	Neogastropoda	Phasianellidae	Polynomial	0.998	$W = -0.0002 + 0.0014 * L - 0.0006 * L^2 + 0.0003 * L^3$
				Dialidae	Quadratic	0.996	$W = 0.0162 - 0.0137 * L + 0.0032 * L^2$
				Potamididae	Quadratic	0.928	$W = 0.1189 - 0.0598 * L + 0.0063 * L^2$
				Buccinidae	Quadratic	0.800	$W = 0.0525 - 0.0413 * L + 0.0080 * L^2$
Arthropoda	Bivalvia	Trochida	Cancellariidae	Quadratic	0.879	$W = 0.0029 - 0.0011 * L + 0.0006 * L^2$	
			Columbellidae	Polynomial	0.909	$W = 0.0479 - 0.0248 * L + 0.0022 * L^2 + 0.0003 * L^3$	
		Limida	Conidae	Polynomial	0.992	$W = -0.1284 + 0.0548 * L - 0.0057 * L^2 + 0.0004 * L^3$	
			Costellariidae	Polynomial	0.967	$W = 0.0008 + 0.0031 * L - 0.0019 * L^2 + 0.0004 * L^3$	
		Malacostraca	Amphipoda	Fasciolaridae	Polynomial	0.993	$W = -0.0018 + 0.0006 * L + 0.0006 * L^2 + 0.00008 * L^3$
				Mitridae	Quadratic	0.896	$W = 0.0062 - 0.0057 * L - 0.0019 * L^2$
		Isopoda	Isopoda	Muricidae	Quadratic	0.730	$W = -0.0454 - 0.0032 * L + 0.0039 * L^2$
				Terebridae	Linear	0.822	$W = -0.0037 + 0.0027 * L$
				Turbinidae	Quadratic	0.973	$W = -0.0940 + 0.0513 * L + 0.0043 * L^2$
				Limidae	Power	0.937	$W = 0.0002 * L^{2.7064}$
	Mytilidae			Quadratic	0.901	$W = 0.0063 - 0.0098 * L + 0.0027 * L^2$	
	Amphipoda*			Quadratic	0.647	$W = 0.0024 - 0.0014 * L + 0.0004 * L^2$	
	Caprellidae			Linear	0.001	$W = 0.0011 * L^{-0.000004}$	
	Anthuridae			Linear	0.620	$W = -0.0008 + 0.0007 * L$	
	Isopoda*			Quadratic	0.457	$W = 0.0019 - 0.0003 * L + 0.0003 * L^2$	
	Joeropsididae			Linear	0.549	$W = 0.0002 + 0.0005 * L$	
	Decapoda	Tanaidacea	Tanaidacea*	Linear	0.188	$W = -0.0007 + 0.0025 * L$	
			Alpheidae	Quadratic	0.881	$W = 0.0234 - 0.0119 * L + 0.0014 * L^2$	
		Decapoda	Diogenidae	Quadratic	0.810	$W = 0.2861 - 0.0635 * L + 0.0067 * L^2$	
			Epialtidae	Quadratic	0.910	$W = 0.0194 - 0.0290 * L + 0.0121 * L^2$	
Majidae		Galatheididae	Quadratic	0.685	$W = -0.0060 + 0.0049 * L + 0.0030 * L^2$		
		Hippolytidae	Polynomial	0.994	$W = 0.0011 + 0.0005 * L - 0.0001 * L^2 + 0.00002 * L^3$		
Paguridae		Majidae	Linear	0.712	$W = -0.0678 + 0.0423 * L$		
		Paguridae	Linear	0.383	$W = -0.0395 + 0.0184 * L$		
Pilumnidae		Palaemonidae	Palaemonidae	Quadratic	0.673	$W = 0.0019 - 0.0016 * L + 0.0004 * L^2$	
			Pilumnidae	Quadratic	0.944	$W = 0.0519 - 0.0437 * L + 0.0099 * L^2$	

Table 2 continued

Phylum	Class	Order	Family	Fit type	R ²	Equation
Echinodermata	Ophiuroidea	Amphiplepidida Ophiacanthida	Portunidae	<i>Quadratic</i>	0.889	$W = -0.0295 - 0.0034 * L + 0.0032 * L^2$
			Tetraliidae	<i>Quadratic</i>	0.941	$W = 0.0329 - 0.0322 * L + 0.0084 * L^2$
			Trapeziidae	<i>Quadratic</i>	0.950	$W = 0.0952 - 0.0657 * L + 0.0124 * L^2$
			Xanthidae	Polynomial	0.945	$W = -0.0173 + 0.0150 * L - 0.0025 * L^2 + 0.0005 * L^3$
			Ophiactidae	Polynomial	0.985	$W = 0.0007 - 0.0013 * L + 0.0024 * L^2 + 0.0006 * L^3$
			Ophiomyxidae	<i>Quadratic</i>	0.918	$W = 0.0290 - 0.0337 * L + 0.0116 * L^2$

Asterisk indicates higher levels of taxonomy; italics indicates alternate model selection; W weight (g); L length (mm)

although microhabitat type significantly influenced the size of one-third of the groups examined. At the community level, live coral hosted fewer but larger individuals, while dead coral and rubble hosted a disproportionate number of small fauna. Over an order of magnitude, more individuals were identified in dead coral than in live *Acropora* and almost 15-fold more in coral rubble. Thus, while the mean weight of motile cryptofauna was greatest in live coral, total biomass is likely to be greatest in dead coral and rubble owing to the sheer number of individuals present. This contributes to the growing understanding that microhabitat structure and type are important determinants of cryptofauna assemblages (Depczynski and Bellwood 2005; Fraser et al. 2020), biomass allocation (Hutchings 1983; Reaka-Kudla 1997; Enochs et al. 2011), ecosystem productivity (Morais et al. 2020) and, likely, trophic pathways (Rogers et al. 2014; Kramer et al. 2016; Rogers et al. 2018a) on coral reefs.

Stepping beyond biodiversity surveys for motile cryptofauna is essential to the characterisation of tractable trophodynamic and ecosystem-based fisheries models that incorporate invertebrate–invertivore pathways. The LWRs presented here provide data on motile cryptofauna to refine food web models from a bottom-up perspective. Models and research regarding coral reef trophodynamics predict that reef degradation profiles—from live to dead coral—may benefit fisheries productivity due to an initial increase in resource availability (e.g. invertebrates and turf algae) (Rogers et al. 2018a; Morais et al. 2020). Our data support this notion through the greater density of motile cryptofauna in dead coral and rubble, although direct trophic links to higher-order taxa (e.g. invertivorous fishes) on coral reefs are poorly described (Wolfe et al. 2019).

Patterns in the cryptofauna among microhabitats are likely to influence invertebrate–invertivore trophic pathways in coral reef ecosystems. For example, the complex morphology of live coral limits prey extraction (Hixon and Jones 2005) and supports a relatively high biomass of coral-associated cryptofauna (Stella et al. 2010, 2011; Kramer et al. 2014). This results in a greater biomass allocation per prey item in live coral, which is largely reserved for species with specialised morphologies that can avail of the complex interstices, such as the bird wrasse, *Gomphosus varius* (Wainwright et al. 2004; Kramer et al. 2014). Somewhat counterintuitively, coral reef invertivores do not preferentially target habitats where invertebrate density and abundance are greatest (i.e. dead coral or rubble), as outlined for wrasses (Kramer et al. 2016). Instead, invertivorous fishes are often opportunistic and forage haphazardly for a diversity of prey across a range of habitats (Fulton and Bellwood 2002; Kramer et al. 2016). These generalist invertivores would require more frequent

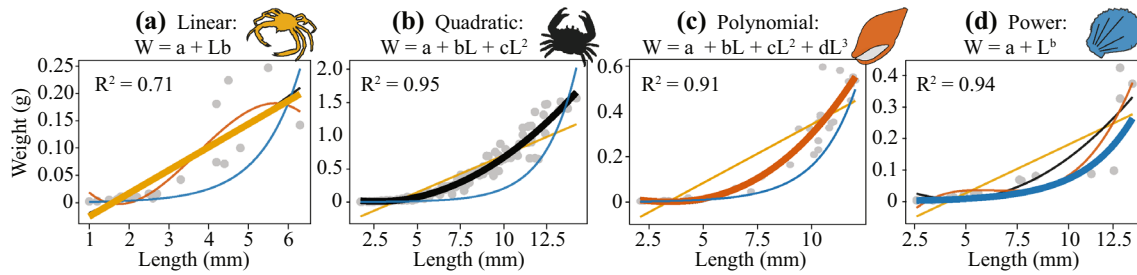


Fig. 1 Length–weight relationships for **a** Majidae ($n = 22$), **b** Trapeziidae ($n = 181$), **c** Columbellidae ($n = 35$) and **d** Limidae ($n = 17$) representing examples of the best-fit models for each model type

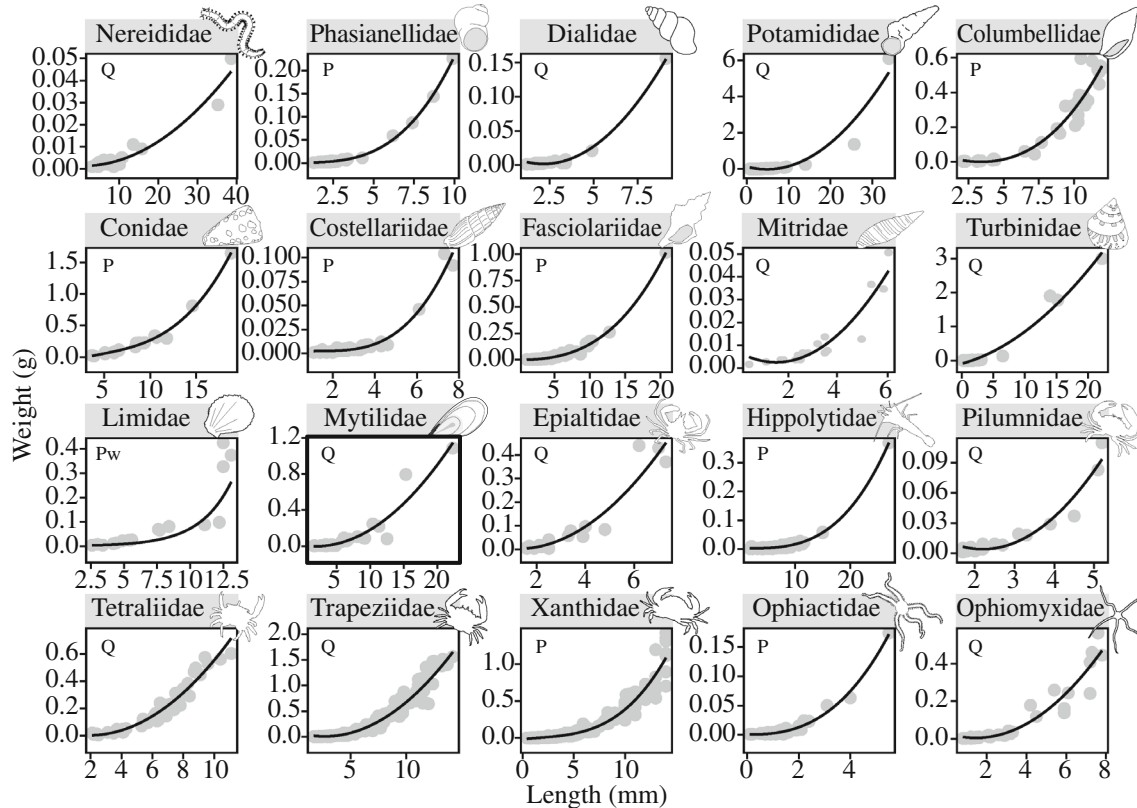


Fig. 2 Length–weight relationships for motile cryptofauna with $R^2 \geq 0.90$. Letters denote relationship fit (*Q* quadratic, *P* polynomial, *Pw* power)

Table 3 Mean (\pm SE) length and weight and total number (n) of motile cryptofauna found in four microhabitats

Habitat	n	Length (mm)	Weight (g)
Live <i>Acropora</i>	126	7.29 ± 0.03	0.19 ± 0.002
Live <i>Pocillopora</i>	411	9.58 ± 0.02	0.40 ± 0.002
Dead coral	1507	4.40 ± 0.002	0.06 ± 0.0003
Rubble	1913	4.64 ± 0.002	0.06 ± 0.0001

success in dead coral and rubble where the relative yield per prey item is likely to be lower.

Biogeography has been shown to influence LWRs in some marine invertebrates (Al-Rashdi et al. 2007; Robinson et al. 2010; Saleky et al. 2016) and fishes (Yamagawa 1994; Blanchard et al. 2005; Joyeux et al. 2009; Jellyman et al. 2013; Ahmed et al. 2015; Ontomwa et al. 2018) owing to differences among seasons, habitats and/or fishing intensity. Here, 13 groups of motile cryptofauna showed significant differences in their size distribution based on microhabitat type. This is an important consideration for future research aiming to characterise habitat-specific LWRs. We acknowledge that the level of detail provided here is mostly to family and that species-specific variation was largely overlooked in our length–weight calculations.

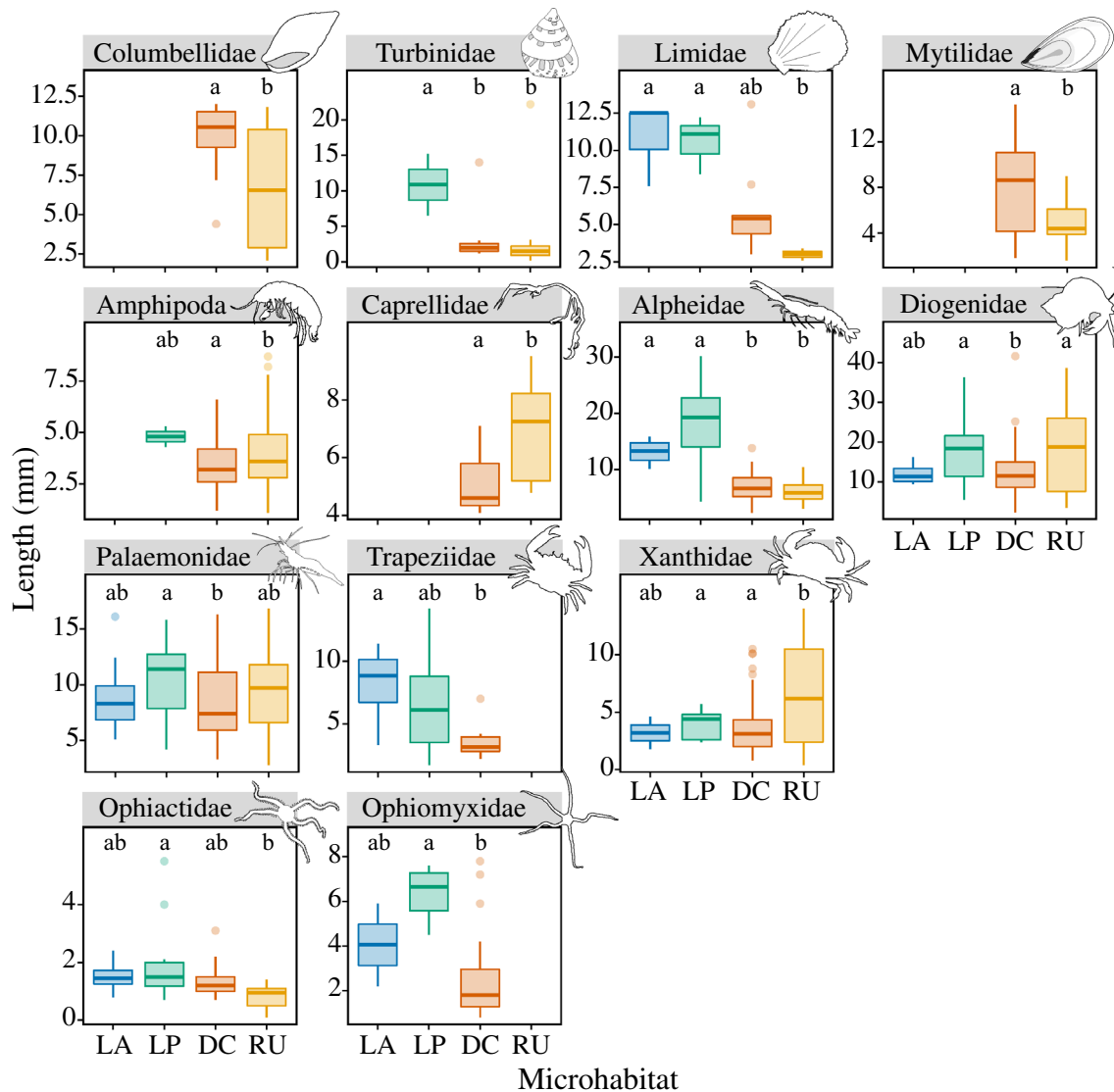


Fig. 3 Box plots showing length (mm) of motile cryptofauna in live *Acropora* (LA), live *Pocillopora* (LP), dead coral (DC) and rubble (RU). Data only shown for groups with a significant effect ($p < 0.05$).

Absent data indicate no individuals were found. Post hoc Tukey’s HSD: letters that are the same do not differ

Thus, it is likely that these differences in size among habitats are a reflection of taxonomy rather than interspecific variation. One exception could be for trapeziid decapods, which are specialised coral associates that generally only move between live corals (i.e. to be found in other microhabitats) as a result of saturated population densities and/or territoriality in their live coral homes (Stella et al. 2011); assumedly, smaller individuals would be forced to move, which is why we found fewer but smaller trapeziids in dead coral. Greater resolution in data, including higher-order classification and increased sample sizes, would improve our ability to differentiate LWRs for speciose groups and disentangle the influence of microhabitat type on cryptofauna size spectra.

As evidenced by the three groups with the—lowest R^2 values in their LWRs (Arthropoda: Caprellidae and Tanaidacea; Polychaeta: Amphinomididae), measurements of length for species with long and skinny morphologies may not be a great indicator of weight. For example, weight of the Caprellidae was consistently low (0.001–0.002 g) despite a relatively broad range in length (4.1–9.5 mm). Incorporation of width–weight measurements may provide an effective method to account for varying and/or disproportionate morphologies in future LWR calculations, as shown among terrestrial insects (Schoener 1980; Sample et al. 1993; Wardhaugh 2013).

We provide the first documentation of LWRs for a series of motile cryptofaunal taxa common in coral reef ecosystems, even at the family level. Given the paucity of data

available for the motile cryptofauna beyond biodiversity censuses, we provide summary information for all 42 groups regardless of the quality of the relationship to ensure these data are carefully considered and to outline where greater attention to detail is needed. We urge caution in the application of the LWRs provided here for several groups with poorly fit models (e.g. Caprellidae), owing to their small size (< 5 mm) and weight (< 0.01 g). In consideration of the high densities typical of motile cryptofauna, ecosystem-level biomass estimates should employ these poor-fit LWRs with care. Moreover, datasets with large individuals beyond the upper size limits used to calculate LWRs here should be wary of overextrapolation, particularly for LWRs defined using polynomial and power models. Regardless, these data can be applied to better understand reef ecosystem functioning and trophodynamics from a novel perspective of reef biodiversity. Greater attention to detail for the cryptofauna in models that address habitat condition, food webs and fisheries productivity on coral reefs will improve our ability to address current patterns and future trajectories as reefs degrade.

The motile cryptofauna are an overlooked group owing to the complexities in identifying, sampling and monitoring their assemblages (Fraser et al. 2020). Availability of LWRs, as presented here, may support and inspire a greater recognition of the cryptofauna on coral reefs, making it more possible for this field of research to expand. With this baseline biometric information, fine-scale underwater surveys could replace the labour-intensive and destructive sampling method currently required to sample certain members of the cryptofauna, most notably for live coral specialists (e.g. Alpheidae, Tetraliidae, Trapeziidae). This would facilitate the estimation of size and species richness without the effort and time of collecting, transporting and processing entire live coral microhabitats. However, identifying and monitoring cryptic individuals in situ remain a significant challenge (Alzate et al. 2014), including through videographic survey methods (Romero-Ramirez et al. 2016; Fraser et al. 2020), particularly in dead coral and rubble where small fauna are abundant.

Acknowledgements We thank the staff of the Palau International Coral Reef Center (PICRC). This study was funded by an ARC Laureate Fellowship and supported by the ARC Centre of Excellence for Coral Reef Studies.

Authors' contributions JS collected the data; KW conceived the idea; AD and KW analysed and interpreted the data; KW wrote the first draft and led writing of the manuscript; all authors contributed to subsequent manuscript drafts.

Compliance with ethical standards

Conflict of interest The authors express no conflict of interest.

References

- Ahmed Q, Ali QM, Bilgin S (2015) Seasonal changes in condition factor and weight-length relationship of tiger perch, *Terapon jarbua* (Forsskål, 1775) (Family-Terapontidae) collected from Korangi Fish Harbour, Karachi, Pakistan. *Pakistan Journal of Marine Sciences* 24:19–28
- Aisyah A, Triharyuni S (2017) Production, size distribution, and length weight relationship of lobster landed in the south coast of Yogyakarta, Indonesia. *Indonesian Fisheries Research Journal* 16:15–24
- Al-Rashdi KM, Claerebout MR, Al-Busaidi SS (2007) Density and size distribution of the sea cucumber, *Holothuria scabra* (Jaeger, 1935), at six exploited sites in Mahout Bay, Sultanate of Oman. *Journal of Agricultural and Marine Sciences* 12:43–51
- Allan D (1974) The relationship between variable selection and prediction. *Technometrics* 16:125–127
- Alzate A, Zapata FA, Giraldo A (2014) A comparison of visual and collection-based methods for assessing community structure of coral reef fishes in the Tropical Eastern Pacific. *Rev Biol Trop* 62:359–371
- Balart EF, Gonzalez-Cabello A, Romero-Ponce RC, Zayas-Alvarez A, Calderon-Parra M, Campos-Davila L, Findley LT (2006) Length-weight relationships of cryptic reef fishes from the southwestern Gulf of California, Mexico. *J Appl Ichthyol* 22:316–318
- Bartoni K (2018) MuMIn: Multi-model inference. R Package Version 1(42):1
- Bascompte J, Melián CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences* 102:5443–5447
- Bellwood DR, Goatley CHR, Bellwood O (2017) The evolution of fishes and corals on reefs: form, function and interdependence. *Biol Rev* 92:878–901
- Bellwood DR, Hughes TP (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292:1532–1534
- Blanchard JL, Dulvy NK, Jennings S, Ellis JR, Pinnegar JK, Tidd A, Kell LT (2005) Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *Ices J Mar Sci* 62:405–411
- Bohnsack J, Harper D (1988) Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean Technical Memorandum NMFS-SEFC-215. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Miami, Florida
- Brandl SJ, Goatley CHR, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Biological reviews of the Cambridge Philosophical Society* 93:1846–1873
- Brandl SJ, Tornabene L, Goatley CHR, Casey JM, Morais RA, Côté IM, Baldwin CC, Parravicini V, Schiettekatte NMD, Bellwood DR (2019) Demographic dynamics of the smallest marine vertebrates fuel coral-reef ecosystem functioning. *Science* 364:1189–1192
- Brey T (1990) Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. *Meeresforschung* 32:329–343
- Brock RE (1982) A Critique of the Visual Census Method for Assessing Coral-Reef Fish Populations. *B Mar Sci* 32:269–276
- Carvalho S, Aylagas E, Villalobos R, Kattan Y, Berumen M, Pearman JK (2019) Beyond the visual: using metabarcoding to characterize the hidden reef cryptobiome. *Proceedings of the Royal Society B: Biological Sciences* 286:20182697

- Cawley GC, Talbot NL (2010) On over-fitting in model selection and subsequent selection bias in performance evaluation. *Journal of Machine Learning Research* 11:2079–2107
- Cohen R, Lough R (1981) Length-weight relationships for several copepods dominant in the Georges Bank-Gulf of Maine area. *Journal of Northwest Atlantic Fishery Science* 2:47–52
- Conand C (1993) Ecology and reproductive biology of *Stichopus variegatus* an Indo-Pacific coral reef sea cucumber (Echinodermata, Holothuroidea). *B Mar Sci* 52:970–981
- Depczynski M, Bellwood DR (2005) Wave energy and spatial variability in community structure of small cryptic coral reef fishes. *Mar Ecol Prog Ser* 303:283–293
- Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-based model of the impacts of bottom trawling on benthic community structure. *Can J Fish Aquat Sci* 59:1785–1795
- Ebert TA, Ford RF (1986) Population ecology and fishery potential of the spiny lobster *Panulirus penicillatus* at Enewetak Atoll, Marshall Islands. *B Mar Sci* 38:56–67
- Edgar GJ (1990) The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *J Exp Mar Biol Ecol* 137:195–214
- Enochs IC (2012) Motile cryptofauna associated with live and dead coral substrates: implications for coral mortality and framework erosion. *Marine Biology* 159:709–722
- Enochs IC, Manzello DP (2012) Species richness of motile cryptofauna across a gradient of reef framework erosion. *Coral Reefs* 31:653–661
- Enochs IC, Toth LT, Brandtneris VW, Afflerbach JC, Manzello DP (2011) Environmental determinants of motile cryptofauna on an eastern Pacific coral reef. *Mar Ecol Prog Ser* 438:105–118
- Fisher R, O’Leary RA, Low-Choy S, Mengersen K, Knowlton N, Brainard RE, Caley MJ (2015) Species richness on coral reefs and the pursuit of convergent global estimates. *Curr Biol* 25:500–505
- Fontaine CT, Neal RA (1971) Length-weight relations for three commercially important penaeid shrimp of the Gulf of Mexico. *T Am Fish Soc* 100:584–586
- Fraser K, Stuart-Smith R, Ling S, Heather F, Edgar G (2020) Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs. *Mar Ecol Prog Ser* 640:31–43
- Froese R (2006) Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J Appl Ichthyol* 22:241–253
- Froese R, Pauly D (2018) FishBase (www.fishbase.org)
- Fulton CJ, Bellwood DR (2002) Patterns of foraging in labrid fishes. *Mar Ecol Prog Ser* 226:135–142
- Ganihar S (1997) Biomass estimates of terrestrial arthropods based on body length. *J Biosciences* 22:219–224
- Glynn PW (2013) Fine-scale interspecific interactions on coral reefs: functional roles of small and cryptic metazoans. *Research and Discoveries: The Revolution of Science through Scuba. Smithsonian Contributions to the Marine Sciences*, pp 229–248
- Gowing G, Recher H (1984) Length-weight relationships for invertebrates from forests in south-eastern New South Wales. *Aust J Ecol* 9:5–8
- Griffiths D (1986) Size-abundance relations in communities. *The American Naturalist* 127:140–166
- Heron AC, McWilliam P, Pont GD (1988) Length-weight relation in the salp *Thalia democratica* and potential of salps as a source of food. *Mar Ecol Prog Ser* 125–132
- Hixon MA, Jones GP (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859
- Hutchings PA (1983) Cryptofaunal communities of coral reefs. In: D.J. B (eds) *Perspectives in coral reefs*, Australian Institute of Marine Science, Townsville, pp 200–208
- Jellyman P, Booker D, Crow S, Bonnett M, Jellyman D (2013) Does one size fit all? An evaluation of length-weight relationships for New Zealand’s freshwater fish species. *New Zeal J Mar Fresh* 47:450–468
- Jennings S, Oliveira JAd, Warr KJ (2007) Measurement of body size and abundance in tests of macroecological and food web theory. *J Anim Ecol* 76:72–82
- Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Mar Ecol Prog Ser* 240:11–20
- Joyeux JC, Giarrizzo T, Macieira R, Spach H, Vaske T Jr (2009) Length-weight relationships for Brazilian estuarine fishes along a latitudinal gradient. *J Appl Ichthyol* 25:350–355
- Klumpp DW, Pulfrich A (1989) Trophic significance of herbivorous macroinvertebrates on the central Great Barrier Reef. *Coral Reefs* 8:135–144
- Kramer MJ, Bellwood DR, Bellwood O (2014) Benthic Crustacea on coral reefs: a quantitative survey. *Mar Ecol Prog Ser* 511:105–116
- Kramer MJ, Bellwood O, Bellwood DR (2016) Foraging and microhabitat use by crustacean-feeding wrasses on coral reefs. *Mar Ecol Prog Ser* 548:277–282
- Kulbicki M, Guillemot N, Amand M (2005) A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybiurn* 29:235–252
- Lee S, Ford A, Mangubhai S, Wild C, Ferse S (2018) Length-weight relationship, movement rates, and in situ spawning observations of *Holothuria scabra* (sandfish) in Fiji. *SPC Beche-de-mer Information Bulletin* 38:11–14
- Lenth R (2019) emmeans: estimated marginal means (least-squares means). R Package Version 1(3):3
- Letourneur Y, Kulbicki M, Labrosse P (1998) Length-weight relationship of fishes from coral reefs and lagoons of New Caledonia: an update. *Naga, the ICLARM Quarterly* 21:39–46
- Madin JS, Anderson KD, Andreasen MH, Bridge TCL, Cairns SD, Connolly SR, Darling ES, Diaz M, Falster DS, Franklin EC, Gates RD, Hoogenboom MO, Huang D, Keith SA, Kosnik MA, Kuo CY, Lough JM, Lovelock CE, Luiz O, Martinelli J, Mizerek T, Pandolfi JM, Pochon X, Pratchett MS, Putnam HM, Roberts TE, Stat M, Wallace CC, Widman E, Baird AH (2016) The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Sci Data* 3
- Morais RA, Depczynski M, Fulton C, Marnane M, Narvaez P, Huertas V, Brandl SJ, Bellwood DR (2020) Severe coral loss shifts energetic dynamics on a coral reef. *Funct Ecol*
- Natan Y, Uneputti PA, Lewerissa Y, Pattikawa J (2015) Species and size composition of sea cucumber in coastal waters of UN bay, Southeast Maluku, Indonesia. *International Journal of Fisheries and Aquatic Studies* 3:251–256
- Odum E (2013) *Methods in ecosystem science*. Springer Science & Business Media, New York
- Otomwa MB, Okemwa GM, Kimani EN, Obota C (2018) Seasonal variation in the length-weight relationship and condition factor of thirty fish species from the Shimoni artisanal fishery, Kenya. *Western Indian Ocean Journal of Marine Science* 17:103–110
- Opitz S (1993) A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem. *Trophic Models of Aquatic Ecosystems* 26:259–267
- Penn J (1980) Observations on length-weight relationships and distribution of the red spot king prawn, *Penaeus longistylus*, in Western Australian waters. *Mar Freshwater Res* 31:547–552

- Peyrot-Clausade M (1979) Contribution to the study of motile reef cryptofauna (Tulear, Madagascar). *Ann I Oceanogr Paris* 55:71–93
- Pitt R, Duy NDQ (2004) Length–weight relationship for sandfish, *Holothuria scabra*. SPC Beche-de-mer Information Bulletin 19:39–40
- Plaisance L, Caley MJ, Brainard RE, Knowlton N (2011) The diversity of coral reefs: What are we missing? *Plos One* 6
- Przeslawski R, Ah Yong S, Byrne M, Worheide G, Hutchings P (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biol* 14:2773–2795
- R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rahman MA, Amin SMN, Yusoff FM, Arshad A, Kuppan P, Nor Shamsudin M (2012) Length weight relationships and fecundity estimates of long-spined sea urchin, *Diadema setosum*, from the Pulau Pangkor, Peninsular Malaysia. *Aquat Ecosyst Health* 15:311–315
- Reaka-Kudla M (1997) The global biodiversity of coral reefs: a comparison with rainforests. In: Reaka-Kudla M, Wilson DE, Wilson EO (eds) *Biodiversity II: understanding and protecting our biological resources*. Joseph Henry Press, Washington, D.C., pp 83–108
- Robinson LA, Greenstreet SPR, Reiss H, Callaway R, Craeymeersch J, de Boois I, Degraer S, Ehrich S, Fraser HM, Goffin A, Kröncke I, Jorgenson LL, Robertson MR, Lancaster J (2010) Length–weight relationships of 216 North Sea benthic invertebrates and fish. *J Mar Biol Assoc Uk* 90:95–104
- Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Curr Biol* 24:1000–1005
- Rogers A, Blanchard JL, Mumby PJ (2018a) Fisheries productivity under progressive coral reef degradation. *J Appl Ecol* 55:1041–1049
- Rogers A, Blanchard JL, Newman SP, Dryden CS, Mumby PJ (2018b) High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. *Ecology* 99:450–463
- Romero-Ramirez A, Gremare A, Bernard G, Pascal L, Maire O, Duchene JC (2016) Development and validation of a video analysis software for marine benthic applications. *J Marine Syst* 162:4–17
- Sakamoto Y, Ishiguro M, Kitagawa G (1986) Akaike information criterion statistics. Dordrecht, The Netherlands: D Reidel 81
- Saleky D, Setyobudiandi I, Toha HA, Takdir M, Madduppa HH (2016) Length-weight relationship and population genetic of two marine gastropods species (Turbinidae: *Turbo sparverius* and *Turbo bruneus*) in the Bird Seascape Papua, Indonesia. *Biodiversitas* 17
- Sample BE, Cooper RJ, Greer RD, Whitmore RC (1993) Estimation of insect biomass by length and width. *American Midland Naturalist*:234–240
- Schoener TW (1980) Length-weight regressions in tropical and temperate forest-understory insects. *Ann Entomol Soc Am* 73:106–109
- Spieß A (2018) qpcR: Modelling and Analysis of Real-Time PCR Data. R package v. 1.4-1
- St John J, Russ GR, Gladstone W (1990) Accuracy and bias of visual estimates of numbers, size structure and biomass of a coral reef fish. *Mar Ecol Prog Ser* 64:253–262
- Stella JS, Jones GP, Pratchett MS (2010) Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* 29:957–973
- Stella JS, Pratchett MS, Hutchings PA, Jones GP (2011) Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology: An Annual Review* 49:43–104
- Takada Y, Abe O, Shibuno T (2007) Colonization patterns of mobile cryptic animals into interstices of coral rubble. *Mar Ecol Prog Ser* 343:35–44
- Takada Y, Abe O, Shibuno T (2012) Variations in cryptic assemblages in coral-rubble interstices at a reef slope in Ishigaki Island, Japan. *Fisheries Sci* 78:91–98
- Tang Y, Horikoshi M, Li W (2016) ggfortify: unified interface to visualize statistical results of popular R packages. *The R Journal* 8:478–489
- Taylor RB (1998) Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Mar Ecol Prog Ser* 172:37–51
- Uye S-i (1982) Length-weight relationships of important zooplankton from the Inland Sea of Japan. *Journal of the Oceanographical Society of Japan* 38:149–158
- Vaitheeswaran T, Jayakumar N, Venkataramani V (2012) Length weight relationship of lobster *Panulirus versicolor* (Latreille, 1804)(Family: Palinuridae) off Thoothukudi waters, southeast coast of India. *Tamilnadu Journal of Veterinary & Animal Sciences* 8:54–59
- Wade B, Fanning L, Auil S (1999) Morphometric relationships for the spiny lobster (*Panulirus argus*) in Belize. *Proceedings of the 45th Gulf and Caribbean Fisheries Institute*:207–213
- Wainwright PC, Bellwood DR, Westneat MW, Grubich JR, Hoey AS (2004) A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol J Linn Soc* 82:1–25
- Wardhaugh CW (2013) Estimation of biomass from body length and width for tropical rainforest canopy invertebrates. *Australian Journal of Entomology* 52:291–298
- Warwick R, Clarke K (1994) Relearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. *Marine Biology* 118:739–744
- Watkins J, Rudstam L, Holeck K (2011) Length-weight regressions for zooplankton biomass calculations—A review and a suggestion for standard equations. *Cornell Biological Field Station Publications and Reports*
- Wilson EO (1992) *The Diversity of Life*. WW Norton, New York
- Wolfe K, Anthony K, Babcock RC, Bay L, Bourne D, Bradford T, Burrows D, Byrne M, Deaker D, Diaz-Pulido G, Frade PR, Gonzalez-Rivero M, Hoey A, Hoogenboom M, McCormick M, Ortiz J-C, Razak T, Richardson AJ, Sheppard-Brennand H, Stella J, Thompson A, Watson S-A, Webster N, Audas D, Beeden R, Bonanno V, Carver J, Chong-Seng K, Cowlshaw M, Dryden J, Dyer M, Groves P, Horne D, Mattocks N, Thiault L, Vains J, Wachenfeld D, Weekers D, Williams G, Mumby PJ (2019) Recommendations to maintain functioning of the Great Barrier Reef. Reef and Rainforest Research Centre Limited, Cairns, Report to the National Environmental Science Programme, p 340
- Yamagawa H (1994) Length-weight relationship of Gulf of Thailand fishes. *Naga, the ICLARM Quarterly* 17:48–52

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.