



New Zealand Journal of Marine and Freshwater Research

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tnzm20

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To cite this article: Marcus M. Key Jr, Abigail M. Smith, Benn Hanns & Pamela Kane-Sanderson (2023) Rare report of bryozoan fouling of rock lobsters (Jasus edwardsii: Decapoda: Palinuridae) from the North Island of New Zealand, New Zealand Journal of Marine and Freshwater Research, 57:2, 229-241, DOI: 10.1080/00288330.2021.1977344

To link to this article: https://doi.org/10.1080/00288330.2021.1977344



Published online: 16 Sep 2021.

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# Rare report of bryozoan fouling of rock lobsters (*Jasus edwardsii*: Decapoda: Palinuridae) from the North Island of New Zealand

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#### ABSTRACT

Bryozoan epibiosis on lobster hosts is rarely reported. Here we document bryozoan fouling of the spiny rock lobster Jasus edwardsii from the Hauraki Gulf, North Island of New Zealand. The 92 lobsters in this study came from the Cape Rodney-Okakari Point Marine Reserve. The lobsters were measured for size and weight, sexed, scanned for epibionts, and photographed. Fortytwo per cent of the lobsters were fouled by epibionts, but only 9% by bryozoans, and they were all males. The bryozoans were all cheilostome gymnolaemates. Only erect colonies were found on the dorsal carapace, and only encrusting colonies were found on the ventral surface. Two of the erect colonies were found in gaping exposed wounds through the exterior wall into the branchial chamber. In addition to host wounds, differences in frequency and location of fouling bryozoan colonies were also attributed to time since last moult and grooming. This epibiosis is interpreted as more of a one-sided commensal symbiotic relationship, perhaps best described as phoretic (i.e. hitchhiking relationship).

ARTICLE HISTORY

Received 10 July 2021 Accepted 2 September 2021

HANDLING EDITOR Richard Taylor

#### **KEYWORDS**

Bryozoa; epibiosis; fouling; rock lobsters; *Jasus edwardsii*; New Zealand

# Introduction

Epibiosis refers to the ecological association between organisms growing attached to a living surface such as the bryozoans on the lobsters in this study. We follow the terminology of Wahl (1989) and refer to the lobsters as basibionts (i.e. the motile host arthropod substrates) and the bryozoans as epibionts (i.e. the sessile organisms attached to the basibiont's outer surface without trophically depending on it).

Fouling refers to the more general colonisation process of a solid surface, living or dead, by epibionts (Wahl 1989). Here we use epibiosis and fouling interchangeably. Some epibionts are opportunists that simply require a hard substrate, others obligate symbionts. Epibiosis is important because fouling epibionts degrade the functionality of ship hulls, heat exchangers and water intake pipes (Hellio and Yebra 2009). Of relevance to this study, the presence of epibionts like bryozoans can cover hosts' eyes,

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inhibit hosts' wound healing, decrease hydrodynamic efficiency of hosts and result in an unappealing appearance of the affected lobster tails (the main consumable part of these lobsters), which lowers their commercial value (Zha et al. 2017).

A variety of organisms can foul the exoskeleton of lobsters. Bryozoans, hydroids, barnacles, serpulid worms, molluscs and many microorganisms can be found growing on the shells of spiny lobsters, but there are few records of their occurrence (Shields 2011). Lobsters often do not have terminal moults, unlike most crabs that do, which keeps fouling rates low (Shields 2011). The objective of this study is to describe a novel occurrence of bryozoan epibiosis on the spiny rock lobster *Jasus edwardsii* (Hutton 1875) in New Zealand, especially by erect colonies on wounded host lobsters.

#### Materials and methods

The basibiont in this study is the palinurid decapod crustacean *J. edwardsii* (Hutton 1875). It is commonly known as the red or spiny rock lobster in New Zealand and the southern rock lobster in Australia. This species is called koura papatea in Maori (Moorfield 2011). It inhabits shallow nearshore rocky reef environments of southern Australia and New Zealand (Kensler 1967; Mislan and Babcock 2008) but also seamounts throughout New Zealand's Exclusive Economic Zone (MacDiarmid and Booth 2003) and the Tasman Sea (Booth 2000). It is cryptic and hides in rock crevices during the day, coming out at night to forage in soft-sediment habitats offshore of their daytime dens (MacDiarmid et al. 1991; Kelly and MacDiarmid 2003).

Catching lobsters is a part of New Zealand history, with Māori considering rock lobster to be historically and culturally significant as well as an important food source. In New Zealand, *J. edwardsii* is the most important lobster species in terms of commercial, recreational and customary fisheries (Woods and James 2003; Breen et al. 2016). The New Zealand rock lobster fishery is primarily based on *J. edwardsii*, which is the most abundant species and contributes to nearly all the landings of commercial catch (Fisheries New Zealand 2019).

The sampled lobsters for this study came from potting surveys in the Hauraki Gulf, 2.5 km north of Leigh on the North Island, New Zealand, in the vicinity of 36.269°S, 174.800°E (Figure 1). In New Zealand, the main method of commercially trapping lobsters is with pots. All were caught in pots in or adjacent to the Cape Rodney-Okakari Point Marine Reserve under the auspices of research permits from the NZ Department of Conservation. This area is characterised by a temperate rocky reef ecosystem dominated by a mix of kelp forest and urchin barrens (Shears and Babcock 2002, 2004). All but five of the lobsters were caught during daily sampling between 6 and 10 August 2019.

Each lobster's weight was measured to the nearest 0.01 kg. Two standard size metrics for this species were measured to the nearest 0.01 mm using digital calipers: (1) Carapace length was measured as the straight-line distance between the eye socket on the rostrum to the posterior edge of the carapace (i.e. the rear margin of the cephalothorax before the tail) on a line parallel to the midline of the body. (2) Tail width was measured as the straight-line distance between the tips of the second abdominal segment. The number of prior injuries was counted on each lobster. A prior injury is one that occurred before being caught and exhibited evidence of healing such as



**Figure 1.** Locality map showing where the lobsters were caught in the Cape Rodney-Okakari Point Marine Reserve, North Island, New Zealand. Modified from Geange et al. (2019, Figure 1).

regenerating missing appendages or scar development on the carapace. Finally, the dorsal and ventral surfaces of each lobster were photographed for epibionts before being released unharmed back to the sea.

The photographs were visually examined for macroscopic epibionts. All macroscopic epizoans, including bryozoans, were identified and the number of each kind counted, and its location recorded. To estimate the age of the bryozoan colonies in order to constrain the time since last moult of the host lobsters, we quantified the size of each bryozoan colony. For encrusting bryozoan colonies, we counted the number of zooids. For erect colonies, we measured their height to the nearest 1 mm. Key's (2020) power function growth curve model was used to estimate colony age in encrusting cheilostomes based on the number of zooids in the colony. Growth rate data from Smith (1992) were used to estimate colony age in erect cheilostomes based on colony height.

#### Results

A total of 92 live *J. edwardsii* lobsters were caught and examined for this study. They ranged in size from 0.37 to 2.86 kg ( $\bar{x}$ : 1.26 kg,  $\sigma$ : 0.59 kg), with tail widths of 55 to 90 mm ( $\bar{x}$ : 74 mm,  $\sigma$ : 8 mm), and carapace lengths of 93 to 171 mm ( $\bar{x}$ : 130 mm,  $\sigma$ : 22 mm). Of the 92 lobsters, 59% were males and 41% females. On average, the males were larger than the females in tail width, carapace length and total weight (Figure 2). Thirty-five per cent of the lobsters had a prior injury, and of those, the number of injuries ranged from 1 to 4. The wounds in the dorsal carapace shown in Figure 3 were through the exterior walls of the branchial chambers. We do not know when these injuries occurred, but they probably happened when the animals were in ecdysis or late postmoult when the carapaces were still somewhat soft. The melanization and wound healing (Theopold et al. 2004) indicate the wounds had been there for some time.

Of the 92 lobsters, 42% were fouled. Male lobsters were 13 times more likely to be fouled (69%) than females (5%). A total of 480 epibionts were found including the polychaete worms *Salmacina* sp. and spirorbine serpulids, balanomorph barnacles, the compound ascidian *Botryllus tuberatus*, as well as the cheilostome bryozoans *Caberea* sp. cf. *zelandica* and one or more unidentified encrusting anascan species (Figures 3–4). The most common epibiont was *Salmacina* sp. with 233 occurrences (49% of 480 total), followed by *Botryllus tuberatus* (22%), spirorbine serpulids (21%), balanomorph barnacles (5%) and the bryozoans (4%). Of the 92 lobsters, 23% had their dorsal surface fouled and 26% of the ventral surfaces. Of the 480 epibionts, 45% were found on the dorsal surface and 55% on the ventral surface.

Only eight (9%) of the lobsters were fouled by bryozoans, and they were all males (Table 1). The bryozoans were all cheilostome gymnolaemates and included four erect colonies of *Caberea* sp. cf. *zelandica* and 12 unidentified anascan encrusting colonies (Table 2). All the erect colonies were found on the dorsal surface, in particular the carapace (Table 2). Half of the erect colonies were found in exposed gaping wounds through the exterior wall into the branchial chamber (Figure 3). All of the encrusting colonies were found on the ventral surface, including the pleurons, uropods and pleopods (Figure 4).

The 12 encrusting anascan colonies averaged 36 zooids in size (range: 1–120 zooids,  $\sigma$ : 39 zooids). Based on the number of zooids in the colony (Key 2020), mean colony age



**Figure 2.** Size distribution of male and female *Jasus edwardsii* lobster specimens used in this study. Males were on average larger in tail width (A), carapace length (B) and weight (C) compared to females.



**Figure 3.** Erect colonies of the cheilostome bryozoan *Caberea* sp. cf. *zelandica* circled in red and growing in exposed wounds in the dorsal carapaces of male *Jasus edwardsii* lobster specimens 1418 (A) and 226 (B) from Hauraki Gulf, New Zealand.

was 8 days (range: 2–17 days,  $\sigma$ : 5 days) (Table 2). Using only the largest colony on each lobster, as opposed to the mean colony size per lobster, better constrains the time since the last moult. Using the largest colony on each lobster, the age range of the colonies was 4–17 days ( $\bar{x}$ : 11 days,  $\sigma$ : 5 days).

The four erect *Caberea* sp. cf. *zelandica* colonies averaged 6 mm in height (range: 3–10 mm,  $\sigma$ : 3 mm). We used Smith's (1992) experimental data on the colony growth rate of a newly settled erect colony of *Caberea zelandica* in the Leigh Marine Reserve to estimate age. In 9 months, the colony grew to a height of 10.0 mm (Smith 1992). This equates to a growth rate of 13 mm/year. Applying this to our erect colonies yields a mean colony age of 168 days (range: 84–281 days,  $\sigma$ : 77 days).

## Discussion

This is the first and only study to report the incidence of bryozoan fouling of *J. edwardsii*, so we do not know if the 9% rate is typical. The 42% of lobsters in



**Figure 4.** Epibionts encrusting the ventral surface of the tail of male *Jasus edwardsii* lobster specimen 1176 from Hauraki Gulf, New Zealand: (**A**) compound ascidian *Botryllus tuberatus*, (**B**) balanomorph barnacle, (**C**) polychaete worm *Salmacina* sp. and (**D**) two unidentified encrusting bryozoan colonies.

Specimen number	Sex	Date caught	Latitude (°S)	Longitude (°E)	Number of prior injuries	Tail width (mm)	Carapace length (mm)	Weight (kg)
226	male	18 July 2014	36.2722	174.8136	1	80.5	171	-
1115	male	07 August 2019	36.2681	174.8020	0	80.51	156.13	2.07
1176	male	09 August 2019	36.2630	174.7935	4	82.5	156.5	2.03
1216	male	09 August 2019	36.2675	174.8098	0	64	113	0.79
1231	male	10 August 2019	36.2662	174.7860	0	70	127	1.06
1236	male	10 August 2019	36.2615	174.7727	0	64	111.5	0.72
1237	male	10 August 2019	36.2615	174.7727	0	75.5	141	1.62
1418	male	21 November 2019	36.2717	174.8199	1	65.75	118.16	0.93
				Count:	8	8	8	8
				Minimum:	0	64	111.5	0.72
				Mean:	0.8	72.8	136.8	1.32
			Maximum:		4	82.5	171	2.07
			Standard deviation:		1	7.4	21.2	0.54

Table 1. Characteristics of the Jasus edwardsii lobsters in this study fouled by bryozoans.

this study that were fouled by any epibiont is lower than McKoy's (1983) report of 70%-80% of *J. edwardsii* off the South Island being fouled by barnacles, but none by bryozoans. Our lower fouling rate is probably a function of the timing of sampling,

Specimen number	Bryozoan	Zoarial habit	General location on host	Specific location on host	Colony size (number of zooids if encrusting, height (mm) if erect)	Mean estimated colony age (days)
226	Caberea sp. cf. zelandica	erect	dorsal	carapace <sup>a</sup>	10	281
1216	Caberea sp. cf. zelandica	erect	dorsal	carapace	7	197
1231	Caberea sp. cf. zelandica	erect	dorsal	carapace	4	112
1418	Caberea sp. cf. zelandica	erect	dorsal	carapace <sup>a</sup>	3	84
1115	unidentified anascan	encrusting	ventral	pleuron	120	17
1115	unidentified anascan	encrusting	ventral	pleuron	100	15
1115	unidentified anascan	encrusting	ventral	pleuron	40	10
1176	unidentified anascan	encrusting	ventral	uropod	65	13
1176	unidentified anascan	encrusting	ventral	uropod	30	9
1236	unidentified anascan	encrusting	ventral	pleopod	47	11
1236	unidentified anascan	encrusting	ventral	pleopod	9	5
1236	unidentified anascan	encrusting	ventral	pleopod	5	4
1237	unidentified anascan	encrusting	ventral	pleopod	4	4
1237	unidentified	encrusting	ventral	pleopod	3	3
1237	unidentified	encrusting	ventral	pleopod	2	3
1237	unidentified anascan	encrusting	ventral	pleopod	1	2

Table 2. Characteristics of the epizoic cheilostome bryozoans fouling *Jasus edwardsii* lobsters in this study.

<sup>a</sup>In an exposed wound through the exterior wall into the branchial chamber.

Table 3.	Month of	sampling	of the <i>Jasu</i>	s edwardsii	lobsters i	n this	study by	/ sex and	proportion	fouled
by any ep	oibiont.									

Month caught	Number of males sampled	Number of females sampled	Proportion of males fouled	Proportion of females fouled
January	0	0		
February	0	0		
March	1	0	0	
April	0	0		
May	0	0		
June	0	0		
July	1	0	100	
August	51	36	69	0
September	0	0		
October	0	0		
November	1	2	100	100
December	0	0		

with ours being earlier in the moult cycle than McKoy's. Southern *J. edwardsii* populations typically moult later than northern populations (Annala & Bycroft 1988; MacDiarmid 1989).

#### Host size and fouling

According to the Target Area Hypothesis (Lomolino 1990), larger lobsters should be more fouled by epibionts, including bryozoans. This hypothesis, derived from MacArthur & Wilson's (1967) Theory of Island Biogeography, argues that larger targets (e.g. islands or the exoskeletons of lobsters) should have more epibionts simply because they are a larger target for 'propagules' (Stracey & Pimm 2009). Based on *t*tests, the lobsters fouled by bryozoans were not significantly larger in tail width (P =0.663, *t*-stat = -0.453, d.f. = 8), carapace length (P = 0.37, *t*-stat. = 0.9319, d.f. = 8), or total weight (P = 0.780, *t*-stat. = 0.290, d.f. = 7), than those not fouled by bryozoans (Figure 2). Marine arthropod basibionts fouled by bryozoans vary in the target area by three orders of magnitude (Key et al. 2013, tbl. 10.2). The target area effect has been consistently documented on a variety of basibionts fouled by bryozoans (Key & Barnes 1999; Key et al. 1995, 1996, 2000, 2013, 2017). So, if the bryozoan-fouled lobsters are not larger, why are they fouled?

#### Host sex and fouling

Perhaps the frequency of fouling is a function of the sex of the lobsters. Male lobsters were 13 times more likely to be fouled than females by any epibiont. Not a single female lobster was fouled by a bryozoan. This might partly be due to egg bearing among the females. Of the females, 95% were carrying eggs when caught, which limits access by settling larvae to the tail's ventral surface.

The higher frequency of fouling of male lobsters may be due to differences in grooming behaviour discussed below. The effectiveness and/or frequency of host grooming is inversely proportional to the number of epibionts (Bauer 1981). It may be, because females carry newly deposited eggs under their tail for 3–5 months, and during this time the female grooms them using a special grooming claw on its 5th pereiopod (NZ SITO 2005).

The higher frequency of fouling of males lobsters is likely also a function of time since their last moult as epibiont load increases with time in decapods (Gili et al. 1993; McGaw 2006). In northern New Zealand, *J. edwardsii* males typically moult in October, whereas females moult late April to early June (MacDiarmid 1989, Figure 2). Of the 92 lobsters in this study, 95% were caught in August (Table 3). Thus, it would have been on average 10 months since the males' last moult as opposed to 3 months for females. This > 3-fold difference in timing is undoubtedly partly responsible for the males' increased incidence of fouling.

#### Host injuries and fouling

The lobsters fouled by bryozoans had on average twice as many prior injuries ( $\bar{x}$ : 0.8 injuries per host) than the rest of the lobsters ( $\bar{x}$ : 0.4 injuries per host). A large wound could impose two functional restraints on a recovering animal affecting its ability to moult or to groom itself. First, other species of spiny lobsters exhibit a 50% increase in their intermoult period when injured (Davis 1981). Perhaps the injured lobsters are more fouled because it has been long since they last moulted. Second, perhaps injured lobsters are

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less able to groom themselves and keep larvae from settling, as is characteristic of many decapods (Bauer 1981). *J. edwardsii* cleans its carapace and abdomen with its pereiopods (Oliver et al. 2008).

The very presence of epibionts is a useful indicator of the health of their host. The New Zealand seafood industry uses the presence of epibionts on the carapace of *J. edwardsii* to tell if a lobster is sick (NZ SITO 2005). Perhaps the injury creates a substrate with a surface texture that is more conducive to bryozoan larval settlement. It is noteworthy that the two lobsters with exposed wounds in the carapace both housed erect bryozoan colonies. The relationship between carapace wounds and fouling bryozoans is supported by another specimen of *J. edwardsii* not included in this study. It was from the Alderman Islands, New Zealand and was photographed by a SCUBA diver on 27 October 2012. It had a similar wound on its carapace that appeared to have erect crisiid cyclostome bryozoan colonies growing in and around the wound.

#### Host moulting frequency and fouling

The frequency of host moulting is inversely proportional to the time since the last moult and the number of epibionts (Gili et al. 1993; Fernandez-Leborans 2010). Since fouling can become established only during interecdysal periods, the bryozoan larvae settled sometime between the previous moult and the time of capture. The presence of epibionts on *J. edwardsii* lobsters is indicative of late intermoult to late premoult stages of its moult cycle (Musgrove 2000). The frequency of moulting decreases with increasing age and size in *J. edwardsii* (Musgrove 2000). *J. edwardsii*, like most lobsters, does not have a terminal moult following attainment of sexual maturity and mating (Phillips et al. 1980). As a result, it continues to moult throughout its life, just less frequently. Thus, epibionts continue to be discarded throughout its life. Diggles and Nadlinger (1999) noted that epibionts on *J. edwardsii* gradually increase over time with increasing time since the last moult. We observed this phenomenon between the male and female lobsters in this study as discussed above.

Erect bryozoan colonies were restricted to the dorsal surface and were older ( $\bar{x}$ : 168 days). Encrusting colonies were restricted to the ventral surface and were younger ( $\bar{x}$ : 11 days). Why was the erect colony age estimates an order of magnitude greater than for the encrusting colonies when the time since last moult was the same for both? The erect colony ages were within the range of the intermoult duration in *J. edwardsii* of 78–287 days (Musgrove 2000) as would be expected for an epibiont on a moulting host. The encrusting colony ages on the ventral surfaces were much younger than this. This may reflect abrasion of ventral colonies and/or host grooming of the ventral surfaces, as discussed above. Alternatively, it may be a function of the different timing of larvae release by the erect and encrusting species.

#### Host exoskeleton characteristics and fouling

Characteristics of a host's exoskeleton (e.g. surface roughness, wettability and microbial film) affect the number of epibionts (Wahl 1989). This may explain why there were three times as many bryozoan colonies on the ventral surface as compared to the dorsal surface (Table 2). In addition, all the ventral colonies were encrusting,

and the dorsal colonies were all erect (Table 2). Compared to the ventral surface, the host's dorsal carapace has an extremely rough surface texture (Figures 3–4) that may deter encrusting colonies.

#### Summary of host characteristics that influence fouling rate

Our data indicate that the three main characteristics of the host lobster that affect bryozoan fouling rate are sex, presence of injuries and time since the last moult. The lobsters that were most likely to be fouled by bryozoans were males with more pre-existing injuries and more time had lapsed since their last moult.

The key for a successful epibiotic relationship, from the bryozoan perspective, is that the epibiont must reach reproductive maturity in less time than it takes for the basibiont to complete its moult cycle. Were the bryozoan colonies big enough to have sexually reproduced to make this host lobster basibiont a viable substrate? There is no data relating erect colony size to the timing of sexual maturity, and no ovicells or embryos were visible on the colonies. But there is such data for encrusting cheilostome species, and it ranges widely. For example, many interstitial species reach sexual maturity by < 10 zooids, *Drepanophora* sp. by 30 zooids, *Parasmittina* sp. and *Stylopoma spongites* by 150 zooids, but *Stylopoma* sp. not until it has 4600 zooids (Jackson and Wertheimer 1985; Winston and Hakansson 1986; Herrera et al. 1996). The encrusting colonies were 1–120 zooids in size ( $\bar{x}$ : 36 zooids,  $\sigma$ : 39 zooids) (Table 2). Thus, it is unlikely that all of these bryozoan colonies reached sexual maturity. Thus, the relationship with their host would be better described as commensalism. Overall, this is a onesided commensal symbiotic relationship, best described as phoretic (i.e. hitchhiking relationship).

#### Acknowledgments

We thank the staff and students at the Leigh Marine Research Laboratory, NZ for help with the field work. J. Shields (Virginia Institute of Marine Science, USA) helped with lobster wound interpretation. D. Gordon (National Institute of Water and Atmospheric Research, NZ) helped with bryozoan identifications. Thanks to the two anonymous reviewers whose comments greatly improved the manuscript.

#### **Disclosure statement**

No potential conflict of interest was reported by the author(s).

## Funding

This work was supported by an Oceans of Change grant from the Department of Conservation.

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#### References

- Annala JH, Bycroft BL. 1988. Growth of rock lobsters (*Jasus edwardsii*) in fiordland, New Zealand. New Zealand Journal of Marine and Freshwater Research. 22(1):29–41.
- Bauer RT. 1981. Grooming behavior and morphology in the decapod crustacea. Journal of Crustacean Biology. 1(2):153-173.
- Booth JD. 2000. New Zealand's rock lobster fisheries. In: Phillips BF, Kittaka J, editors. Spiny lobsters: fisheries and culture. Oxford: Blackwell Science. p. 78–89.
- Breen PA, Branson AR, Bentley N, Haist V, Lawson M, Starr PJ, Sykes DR, Webber DN. 2016. Stakeholder management of the New Zealand Red Rock lobster (*Jasus edwardsii*) fishery. Fisheries Research. 183(11):530–538.
- Davis GE. 1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fishery Bulletin. 78(4):979–984.
- Diggles BK, Handlinger J. 1999. Disease conditions of larval and juvenile spiny lobsters. In: Evans LH, editor. Rock lobster autopsy manual. Adelaide: Curtin University; p. 68–85.
- Fernandez-Leborans G. 2010. Epibiosis in crustacea: an overview. Crustaceana. 83(5):549-640.
- Fisheries New Zealand. 2019. Fisheries assessment plenary, November 2019: stock assessments and stock status. Compiled by the fisheries science and information group. Wellington, NZ: Fisheries New Zealand.
- Geange S, Townsend M, Clark D, Ellis JI, Lohrer AM. 2019. Communicating the value of marine conservation using an ecosystem service matrix approach. Ecosystem Services. 35:150–163.
- Gili J-M, Abello P, Villanueva R. 1993. Epibionts and intermoult duration in the crab *Bathynectes piperitus*. Marine Ecology Progress Series. 98(1–2):107–113.
- Hellio C, Yebra D. 2009. Advances in marine antifouling coatings and technologies. Oxford: Woodhead Publishing, p. 784.
- Herrera A, Jackson JBC, Hughes DJ, Jara J, Ramos H. 1996. Life-history variation in three coexisting cheilostome bryozoan species of the genus *Stylopoma* in panamá. Marine Biology. 126:461–469.
- Hutton FW. 1875. Descriptions of two new species of Crustacea from New Zealand. Annals and Magazine of Natural History, Series 4. 15(85):41–42.
- Jackson JBC, Wertheimer SP. 1985. Patterns of reproduction in five common species of Jamaican reef-associated bryozoans. In: Nielsen C, Larwood GP, editors. Bryozoa: ordovician to recent. Fredensborg: Olsen & Olsen; p. 161–168.
- Kelly S, MacDiarmid AB. 2003. Movement patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. New Zealand Journal of Marine and Freshwater Research. 37(1):149–158.
- Kensler CB. 1967. The distribution of spiny lobsters in New Zealand waters (Crustacea: Decapoda: Palinuridae). New Zealand Journal of Marine and Freshwater Research. 1(4):412–420.
- Key Jr MM. 2020. Estimating colony age from colony size in encrusting cheilostomes. In: Wyse Jackson P, Zágoršek K, editors. Bryozoan studies 2019. Prague: Czech Geological Society; p. 83–90.
- Key Jr MM, Barnes DKA. 1999. Bryozoan colonization of the marine isopod *Glyptonotus antarcticus* at Signy Island, Antarctica. Polar Biology. 21(1):48–55.
- Key MM, Hyžný M, Khosravi E, Hudáčková N, Robin N, Mirzaie Ataabadi M. 2017. Bryozoan epibiosis on fossil crabs: a rare occurrence from the miocene of Iran. Palaios. 32(8):491–505.
- Key Jr MM, Jeffries WB, Voris HK. 1995. Epizoic bryozoans, sea snakes, and other nektonic substrates. Bulletin of Marine Science. 56(2):462–474.
- Key Jr MM, Jeffries WB, Voris HK, Yang CM. 1996. Epizoic bryozoans and mobile ephemeral host substrata. In: Gordon DP, Smith AM, Grant-Mackie JA, editors. Bryozoans in space and time. Wellington: National Institute of Water and Atmospheric Research; p. 157–165.
- Key Jr MM, Jeffries WB, Voris HK, Yang CM. 2000. Bryozoan fouling pattern on the horseshoe crab *Tachypleus gigas* (Müller) from Singapore. In: Herrera Cubilla A, Jackson JBC, editors. Proceedings of the 11th International Bryozoology Association conference; Jan 26-31, 1998; Balboa. Balboa (PA): Smithsonian Tropical Research Institute; p. 265–271.
- Key Jr MM, Knauff JB, Barnes DKA. 2013. Epizoic bryozoans on predatory pycnogonids from the south orkney islands, Antarctica: 'If you can't beat them, join them'. In: Ernst A, Schäfer P, Scholz J, editors. Bryozoan studies 2010. Berlin: Springer-Verlag; p. 137–153.

- Lomolino MV. 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. Oikos. 57(3):297–300.
- MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton (NJ): Princeton University Press.
- MacDiarmid AB. 1989. Moulting and reproduction of the spiny lobster *Jasus edwardsii* (Decapoda: Palinuridae) in northern New Zealand. Marine Biology. 103(3):303–310.
- MacDiarmid AB, Booth JD. 2003. Crayfish. In: Andrew N, Francis M, editors. The living reef: the ecology of New Zealand's rocky reefs. Nelson: Craig Potton Publishing; p. 120–127.
- MacDiarmid AB, Hickey B, Maller RA. 1991. Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. Journal of Experimental Marine Biology and Ecology. 147(2):185–205.
- McGaw IJ. 2006. Epibionts of sympatric species of *Cancer* crabs in barkley sound, British Columbia. Journal of Crustacean Biology. 26(1):85–93.
- McKoy JL. 1983. Movements of rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae), tagged near Stewart Island, New Zealand. New Zealand Journal of Marine and Freshwater Research. 17(4):357–366.
- Mislan KAS, Babcock RC. 2008. Survival and behaviour of juvenile Red Rock lobster, *Jasus edwardsii*, on rocky reefs with varying predation pressure and habitat complexity. Marine and Freshwater Research. 59(3):246–253.
- Moorfield JC. 2011. Te Aka Maori-English, English-Maori dictionary and index, 3rd ed. Auckland, NZ: Pearson.
- Musgrove RJ. 2000. Moult staging in the southern rock lobster Jasus edwardsii. Journal of Crustacean Biology. 20(1):44-53.
- [NZ SITO] New Zealand Seafood Industry Training Organization. 2005. Biology of a species of aquatic crustacean, Red Rock lobster (*Jasus edwardsii*) learning resource for unit standard 20306. Wellington: New Zealand Seafood Industry Training Organization.
- Oliver MD, MacDiarmid AB, Stewart RA, Gardner C. 2008. Anti-predator behavior of captive-reared and wild juvenile spiny lobster (*Jasus edwardsii*). Reviews in Fisheries Science. 16(1):186–194.
- Phillips BF, Cobb JS, George RW. 1980. General biology. In: Cobb JS, Phillips BF, editors. The biology and management of lobsters. vol. I, physiology and behavior. New York, NY: Academic Press; p. 1–82.
- Shears NT, Babcock RC. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia. 132(1):131–142.
- Shears NT, Babcock RC. 2004. Community composition and structure of shallow subtidal reefs in northeastern New Zealand. Wellington: NZ DOC.
- Shields JD. 2011. Diseases of spiny lobsters: a review. Journal of Invertebrate Pathology. 106(1):79-91.
- Smith AM. 1992. Aspects of the sedimentology of New Zealand bryozoans and mixed carbonateclastic deposits: a contribution to the temperate shelf carbonate model [dissertation]. Waikato (NZ): University of Waikato.
- Stracey CM, Pimm SL. 2009. Testing island biogeography theory with visitation rates of birds to British islands. Journal of Biogeography. 36(8):1532–1539.
- Theopold U, Schmidt O, Söderhäll K, Dushay MS. 2004. Coagulation in arthropods: defence, wound closure and healing. Trends in Immunology. 25(6):289–294.
- Wahl M. 1989. Marine epibiosis. 1. Fouling and antifouling some basic aspects. Marine Ecology Progress Series. 58(1-2):175-189.
- Winston JE, Håkansson E. 1986. The interstitial fauna of the Capron Shoals, Florida. American Museum Novitates. 2865:1–98.
- Woods CMC, James PJ. 2003. Evaluation of visible implant fluorescent elastomer (VIE) as a tagging technique for spiny lobsters (*Jasus edwardsii*). Marine and Freshwater Research. 54 (7):853–858.
- Zha H, Lewis G, Alfaro A, Wang S, Dong Y, Grandiosa R, Jeffs A. 2017. Immune status of the spiny lobster *Jasus edwardsii* with tail fan necrosis. Diseases of Aquatic Organisms. 126(3):229–238.