CSIRO PUBLISHING

Marine and Freshwater Research, 2015, **66**, 981–988
http://dx.doi.org/10.1071/MF14306

New opportunities for conservation of a threatened biogenic habitat: a worldwide assessment of knowledge on bivalve-reef representation in marine and coastal Ramsar Sites

Tim Kasoar[A,B,E], *Philline S. E. zu Ermgassen*[A,B], *Alvar Carranza*[C], *Boze Hancock*[D] and *Mark Spalding*[B]

[A]Department of Zoology, University of Cambridge, Cambridge, CB2 3EJ, UK.
[B]The Nature Conservancy Global Marine Team, Department of Zoology, University of Cambridge, Cambridge, CB2 3HU, UK.
[C]Centro Universitario Regional Este-CURE, Universidad de la República, 20400 Maldonado, Uruguay and Area Biodiversidad y Conservación, Museo Nacional de Historia Natural, 11000 Montevideo, Uruguay.
[D]The Nature Conservancy Global Marine Team, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882-1197 USA.
[E]Corresponding author. Email: tak29@cam.ac.uk

Abstract. The present study draws attention to the current state of knowledge of bivalve reef, an important but historically overlooked habitat type. Recent interest has led to the explicit recognition of this habitat type under the Convention on Wetlands of International Importance (the Ramsar Convention), an international treaty that has widespread governmental and scientific involvement. To assess the state of knowledge, the Information Sheet on Ramsar Wetlands (RIS) for marine and coastal Sites was searched for evidence that bivalve-reef habitat is present in the site. We then examined the quality of this information using alternative data sources. These were public databases of geolocated species records at three spatial scales, local and regional experts, and a general web search. It was found that of the 893 marine and coastal Ramsar Sites considered, the RIS for 16 Sites provided strong evidence of bivalve-reef habitat and 99 had confirmed presence of reef-forming bivalves, a strikingly high number, given that it is not yet compulsory to include bivalve reef in RISs. However, the alternative information sources identified bivalve reefs or reef-forming bivalves in 142 further Sites. No one information source provided comprehensive information, highlighting the overall poor state of knowledge of this habitat type.

Additional keywords: coastal habitats, marine habitats, mussel beds, oyster reefs, shellfish.

Received 1 October 2014, accepted 30 November 2014, published online 9 April 2015

Introduction

Bivalve reef is an ecologically and economically important habitat, but its significance is rarely recognised by the wider scientific community (Carranza *et al.* 2009). Bivalve reefs provide a wide array of ecosystem services, including provisioning, shoreline protection and cultural services. By filtering particles out of the water column and concentrating them in the surrounding sediments, bivalves can significantly influence nutrient cycling and simultaneously increase water clarity (Newell 2004; Ruesink *et al.* 2005). In addition, the structured habitat formed by a reef can act as a nursery for other marine organisms, the shells provide a hard substrate for benthic organisms to attach, and the biodeposits resulting from filtration provide nutrients, thereby increasing local biodiversity (Prins *et al.* 1997; Borthagaray and Carranza 2007; Norling and Kautsky 2007) and fisheries productivity (Peterson *et al.* 2003). Emergent or shallow reefs can also serve to protect shorelines from erosion (Scyphers *et al.* 2011). Furthermore, sustainable harvesting of bivalves can provide food, building material and jewellery, which can be consumed locally or sold to provide an income (Coen *et al.* 2007). Bivalve reefs can, therefore, be extremely valuable; the economic value of the full suite of ecosystem services derived from unharvested oyster reefs in North America was recently estimated to be as high as US\$99 000 ha^{-1} $year^{-1}$ (Grabowski *et al.* 2012), which is notably higher than estimates for other habitat types (e.g. US$60 400 for mangroves, Balmford *et al.* 2002; US$22 832 for estuaries, Costanza *et al.* 1997; US$14 785 for permanent wetlands, Sutton and Costanza 2002).

Bivalve reef is a globally threatened habitat, with an estimated 85% loss of oyster reefs globally from historical abundance (Beck *et al.* 2011) and significant but unquantified losses of other reef-forming bivalves (e.g. Beck *et al.* 2009; Marencic and de Vlas 2009). This has primarily been driven by widespread and intensive harvesting of oysters and mussels for food, combined with pressure from coastal development, anoxia, sedimentation, disease, ocean acidification and non-native species (Gazeau *et al.* 2007; Carranza *et al.* 2009; Beck *et al.* 2011, 2009).

These well documented declines and concurrent loss in ecosystem services have led organisations, including The Nature Conservancy and NOAA, to seek to increase awareness of the ecological and socioeconomic impacts of the decline of bivalve-reef habitats (Beck *et al.* 2009). The recent formal recognition of bivalve reef as a distinct wetland habitat type within the Convention on Wetlands of International Importance, known as The Ramsar Convention, is considered an outstanding step towards the conservation and sustainable use of these habitats.

Under the Convention, contracting parties are obliged to maintain the ecological character of a site (Ramsar Convention 1971), and to that end, an accurate description of the features of the site is critical to ensure appropriate conservation and management. Description of a site is achieved using the Information Sheet on Ramsar Wetlands (RIS), which includes a list of specific habitat types that could occur within the site. The designated authority is required to note the presence and extent of all wetland types listed. Since 2012, 'bivalve (shellfish) reef' has been included among this list (COP11, see http://www.ramsar.org/sites/default/files/documents/pdf/cop11/res/cop11-res08-e.pdf, accessed 10 February 2015). Prior to this amendment, the absence of bivalve reef from the list of habitat types may have contributed to overlooking this habitat type. Its inclusion will, therefore, encourage recognition of the presence of bivalve reef and so improve the conservation and management of those Sites. It also offers the opportunity to designate new Ramsar Sites on the basis of the presence of a representative, rare or unique example of this habitat type (Strategic Framework for the List 2009).

The guidelines provided for identifying and designating particular wetland types (COP11, Appendix E, pp. 91–111 of Resolution XI.8, Annex 2, see http://www.ramsar.org/sites/default/files/documents/pdf/cop11/res/cop11-res08-e-anx2.pdf, accessed 10 February 2015) qualitatively discuss the ecosystem services expected to be provided by bivalve reefs and the importance of protecting both the reef and surrounding areas to maximise the benefits from this provision, but do not include a detailed definition of bivalve-reef habitat. Bearing in mind the need to be globally inclusive and, hence, encompass a range of species and reef characteristics, as well as previous relevant definitions (e.g. Baggett *et al.* 2014), we propose the following definition:

> Bivalve reef consists of large areas of biogenic habitat, dominated by living bivalves where the complex structure of hard shells supports a distinct community that is persistent through time.

Expanding on this general definition: 'large areas' typically consist of multiple patches, at least some of which are larger than 5 m^2; 'dominated' means at least 25% cover of live shell matter across that space – non-living shell (cultch) may further add to habitat structure and to continuity over time, but without new growth they are unlikely to persist; a 'distinct community' is one that supports species and interactions that are rare or absent in surrounding communities; and 'persistent through time' describes communities that are likely to remain over decadal timescales or longer.

The purpose of the present study was to investigate the current status of bivalve reef habitat in Ramsar Sites. To do so, we investigated the extent to which bivalve reef habitat is reported in the current generation of RIS, and to what extent other sources are able to supply these data.

Materials and methods

Identifying study sites

Study sites were identified by searching the Ramsar Sites Information Service (RSIS; Ramsar and Wetlands International 2013) for sites categorised as 'marine and coastal wetlands' or that included any of the following wetland types (as defined in the RIS; COP11, Appendix B, pp. 83–85 of Resolution XI.8, Annex 2, see http://www.ramsar.org/sites/default/files/documents/pdf/cop11/res/cop11-res08-e-anx2.pdf): (A) permanent shallow marine waters, in most cases less than 6 m deep at low tide (includes sea bays and straits); (B) marine subtidal aquatic beds (includes kelp beds, sea-grass beds, tropical marine meadows); (C) coral reefs; (D) rocky marine shores (includes rocky offshore islands, sea cliffs); (E) sand, shingle or pebble shores (includes sandbars, spits and sandy islets; includes dune systems and humid dune slacks); (F) estuarine waters (permanent water of estuaries and estuarine systems of deltas); (G) intertidal mud, sand or salt flats; (H) intertidal marshes (includes salt marshes, salt meadows, saltings, raised salt marshes; includes tidal brackish and freshwater marshes); (I) intertidal forested wetlands (includes mangrove swamps, nipah swamps and tidal freshwater swamp forests); (J) coastal brackish–saline lagoons (brackish to saline lagoons with at least one narrow connection to the sea); and (K) coastal freshwater lagoons (includes freshwater delta lagoons). Although some of these wetland types (particularly C, E and K) are unlikely to be suitable for bivalve reef, the wetland types recorded in the RIS cannot be considered a complete description of a Site and so Sites with only those wetland types recorded have been included. Furthermore, only 41 Sites (5%) contained exclusively those wetland types and removing them would not significantly alter our conclusions.

The RIS for each of these wetlands, where available, was then downloaded from the RSIS (or, for some UK Ramsar Sites, through the JNCC website; JNCC 2006). When multiple versions of RIS were available, the most recent was selected. The RISs were then sorted by language (they can be submitted in English, French or Spanish) and by document type (some were electronic originals; others were scanned copies of hard documents). A small number of documents were supplied in other languages – these were translated into English using Google Translate (see http://translate.google.co.uk, accessed 18 December 2013) then the English keyword list was applied.

Selection of keywords

A list of keywords was developed so as to efficiently capture evidence that bivalve reef is or could be present. The keywords include words related to the habitat (such as 'reef') and taxa known wholly or partly to comprise reef-forming species (e.g. *Ostrea*). The list was developed using a combination of the authors' experience and review of available literature (Beck *et al.* 2009 and references therein). The keywords selected are listed in Table 1. The taxa included in the list also formed the basis for searching the public databases, although not all taxa were available in the databases (see Table 1).

Table 1. List of keywords

English	French	Spanish
Oyster	Huître	Ostra or ostión
Mussel	Moule	Mejillón
Reef	Récif	Arrecife
Bed	Moulière[A]	Ostrero[B]
Shellfish	Coquillages	Marisco or marisquero
Bivalve	Bivalve	Bivalvo
Flame shell or file shell	Lime baillante	Almeja peluda
All languages		
Bivalvia	*Aulacomya*[F]	*Modiolus*[D,F]
Ostreidae	*Mytella*	*Limaria*[D,F]
Mytilidae	*Septifer*[F]	*Isognomon*
Ostrea[D,E,F]	*Ischadium*	*Chama*
Crassostrea[D,F]	*Geukensia*[F]	*Pteria*
Saccostrea	*Brachidontes*[F]	*Pinctada*
Mytilus[D,E,F]	*Modiolarca*[C]	*Tridacna*
Perna	*Gaimardia*	*Atrina*
Choromytilus[F]	*Musculus*[F]	

[A]Specifically refers to mussel beds. References to oyster beds would include the keyword 'huître'.
[B]Specifically refers to oyster beds. References to mussel beds would include the keyword 'mejillon'.
[C]Synonymous with *Gaimardia* (Huber and Gofas 2013) but included for completeness as this name is still sometimes used.
[D]Species in these genera included in UK National Biodiversity Network (UK NBN) database.
[E]Species in these genera included in European Nature Information System (EUNIS) database.
[F]Species in these genera included in Oceanic Biogeographic Information System (OBIS) database.

Ramsar Information Sheets

The electronic originals were searched for keywords by using the built-in search function in Adobe Reader X (Adobe Systems Incorporated, San Jose, CA, USA). When a keyword was found, the RIS was opened so as to read the context and check for other keywords within the same document. Some of the scanned RIS documents have had optical character recognition (OCR) performed, and so all were initially electronically searched in the same way, to rapidly locate documents that contained keywords. In addition, because the OCR process is not perfect and rarely successful at recognising handwriting, all scanned RISs were also reviewed manually for the same keywords.

Each Ramsar Site was classified into five categories (Table 2). Most Sites were assigned to one category; however, when relevant, a Site could be assigned to two (e.g. both 'has reef-forming bivalves' and 'has reef (of unknown origin)'). Wild populations of non-native species (such as *Crassostrea gigas* in parts of North America and Europe) were included. Artificial reefs of farmed bivalves were not included (see Table S1, available as Supplementary material to this paper).

Public databases

From the RIS results, it is impossible to know whether the lack of reported bivalve reef is a true absence or an omission error. To address this, public databases were used as an alternative source of data to compare with the RIS results. A tiered approach was adopted, using databases on national, international and global scales. Because of differences in the presentation of the data and availability of Ramsar information, the three were analysed using slightly different methods. However, all three methods were designed to provide the same output, namely, presence of reef-forming bivalves within Ramsar Sites. Only a subset of the taxa used as keywords were available in each database; these are listed in Table 1.

The national-level database was the UK National Biodiversity Network (UK NBN) (NBN Trust 2013). The UK NBN collates data from a large number of local, regional and national biodiversity recording schemes within the UK. The UK was selected for several reasons. First, the UK NBN is a comprehensive publically available biogeographic database, ideally suited to this type of analysis – a resource that is unavailable in most countries. Second, the UK has a high number (68) of coastal Ramsar Sites, giving a good sample size. Third, all Sites have a GIS boundary shapefile available, so it can be accurately

Table 2. Categories of Information Sheet on Ramsar Wetlands (RIS) sheet and a description of the criteria for each category

Category	Description
Has bivalve reef	RIS contains a clear reference to bivalve reef, or describes the presence of bivalves, which meets our definition of bivalve reef.
Has reef-forming bivalves	Names of one of the taxa known to form reefs as being present in the Site (see Table 1), but no clear reference to the presence of reef or the local density of the species.
Has reef of unknown origin	Has a reference to 'reef' or 'biogenic reef' that could refer to bivalve-formed reef.
Has bivalves of unknown species	Mentions common names (e.g. 'oyster') or higher taxonomic names (e.g. *Bivalvia*) from which it is not possible to determine whether reef-forming species are present.
No evidence of bivalve reef	The RIS contains none of the above. Sites for which no RIS was available are also included in this category.

determined whether or not species records occurred within the Ramsar Site. The UK NBN was searched for occurrence of keyword taxa recorded within the boundaries of Ramsar Sites.

At the international level, the European Union (EU) was chosen because (1) it contains the UK, allowing comparison between national and international levels, (2) Europe has a high number of Ramsar Sites (324) and (3) countries within the EU are subject to a common biodiversity framework established under European legislation, specifically the Birds and Habitats Directives (The Council of the European Communities 1992; The European Parliament and The Council of the European Union 2009). Data for the EU were obtained from the European Nature Information System (EUNIS). EUNIS collates national-level reporting conducted as part of the Natura 2000 framework, which is a network of protected areas, consisting of special protection areas (SPAs) designated under the Birds Directive and special areas of conservation (SACs) designated under the Habitats Directive (Romão *et al.* 2012). There is large overlap between Natura 2000 Sites and Ramsar Sites (DEFRA 2006). As such, for Ramsar Sites also included in the Natura 2000 network, data in EUNIS provide an independent source of information. The data were gathered by using the built-in query function to search for keyword taxa mentioned within the recorded information for all study sites included in EUNIS.

The global dataset used was the Oceanic Biogeographic Information System (OBIS) (OBIS 2013). OBIS, like the UK NBN, is a collation of local biodiversity recording schemes. Note that for the UK, the UK NBN is a more complete compilation, with only a subset of the data providers also contributing to OBIS. OBIS was searched for the presence of the keyword taxa within 5 km of the central point of each Ramsar Site. A distance of 5 km was chosen because that is the default value of precision recorded in OBIS when precision data are not supplied by the original data provider. Furthermore, for many Ramsar Sites, the boundary is not currently available as a GIS shapefile, so the central point was used so as to maximise inclusiveness.

McNemar's test (Everitt 1977) was used to determine whether the evidence provided in each data source differed significantly from the evidence in the RISs, and between the UK NBN and EUNIS. In all cases, it is assumed that there are no false positives, only false negatives. False negatives are likely to occur as a result of poor reporting or a lack of knowledge. Statistical testing was carried out in R (R Core Team 2014).

Expert knowledge

Local and regional experts were contacted by email and in person at the Mollusca 2014 conference. Experts contacted by email were known to the authors as shellfish conservation practitioners or researchers. The experts were asked to state, for any Ramsar Sites with which they were familiar, whether the site had bivalve-formed reef, which bivalves formed this reef, and which (if any) potentially reef-forming bivalves were present at the Site, although not currently forming a reef.

Internet search

The final method was an open internet search. The aim of this search was to quantify false negatives from the other methods combined. As such, 10% of Sites from each region for which none of the other methods had provided evidence for the presence of a bivalve reef or reef-forming bivalves were randomly selected for this analysis. Google Search was searched for '*site name*' and '*site name* mussel OR oyster OR reef' where *site name* was the full name of the Site as given on the RIS (Google Search, see http://www.google.co.uk, accessed 11 August 2014). For Sites in francophone and hispanophone countries, the French or Spanish words for mussel, oyster and reef were used in addition to the English (see Table 1). The first page of the results was reviewed in each case. All searches were carried out between 11 August 2014 and 15 August 2014.

Results

RIS analysis

In total, 893 coastal and marine Ramsar Sites were identified for the study, of which all except 16 had an RIS available. Almost half of the Sites were in Europe, whereas less than 5% were in Oceania. The remaining Sites were spread evenly between Africa, Asia, the Neotropics and North America (9–14% each; Table 3, Fig. 1). Only 16 (2%) Sites had confirmed evidence of a bivalve reef, and 99 (11%) further Sites reported the presence of reef-forming bivalves, which suggests that a bivalve reef could be present (Table 3, Fig. 1). Many of the Sites with bivalves of unknown species were recorded as 'oysters' or 'mussels' (see

Table 3. Evidence of bivalve reef from Information Sheet on Ramsar Wetlands (RIS)

Regions as specified by the Ramsar Sites Information Service (Ramsar and Wetlands International 2013). Sites with no RIS are included in data for 'No evidence'. Rows may sum to over 100% because Sites may be included in more than one category, and because of rounding

Region	Number of Ramsar Sites included	Sites with RIS available (%)	Has bivalve reef (%)	Has reef-forming bivalves (%)	Has reef of unknown origin (%)	Has bivalves of unknown species (%)	No evidence (%)
Africa	120	114 (95)	2 (2)	13 (11)	0 (0)	8 (7)	97 (81)
Asia	104	104 (100)	0 (0)	13 (13)	0 (0)	9 (9)	82 (79)
Europe	423	414 (98)	12 (3)	21 (5)	14 (3)	19 (4)	363 (86)
Neotropics	83	82 (99)	0 (0)	20 (24)	0 (0)	3 (4)	60 (72)
North America	120	120 (100)	2 (2)	28 (23)	0 (0)	10 (8)	80 (67)
Oceania	43	43 (100)	0 (0)	4 (9)	0 (0)	3 (7)	36 (84)
Total	893	877 (98)	16 (2)	99 (11)	14 (2)	52 (6)	718 (80)

Table S1), so there is a strong possibility that in many of these cases, the bivalves are in fact reef-forming species.

Public databases

The UK NBN showed that 52 (76%) of the 68 marine and coastal Ramsar Sites in the UK do have reef-forming bivalves, and in 45 (87%) cases, this was not reflected in the RISs of the Sites. RISs of three sites had evidence for reef-forming bivalves; however, these were not identified by the UK NBN. The evidence provided by the UK NBN is significantly better than that provided by the RISs (McNemar's $\chi^2 = 35.02$, d.f. $= 1$, $P < 0.005$).

Of the 324 study Sites in Europe, EUNIS identified only seven (2%) with reef-forming bivalves. This is significantly worse than the evidence provided by the RISs (McNemar's $\chi^2 = 9.63$, d.f. $= 1$, $P < 0.005$), with EUNIS failing to identify reef-forming bivalves in 24 of 25 Sites identified by RISs. Nevertheless, EUNIS did add to the sum of knowledge on the presence of reef-forming bivalves, identifying six additional Sites not identified by the RISs. It is clear by comparing EUNIS to UK NBN for UK Ramsar Sites that EUNIS is a less complete database (Table S2, available as Supplementary material to this paper) (McNemar's $\chi^2 = 50.02$, d.f. $= 1$, $P < 0.005$). Together, these suggest that EUNIS is likely to be under-reporting across Europe.

Globally, OBIS also identified 107 (12%) of 893 Sites as having reef-forming bivalves, of which 95 Sites were not identified from the relevant RIS description. However, there were also 103 Sites where reef-forming bivalves were reported in the RISs but not in OBIS. Overall, the quality of evidence provided by OBIS is not significantly different from that provided by the RISs (McNemar's $\chi^2 = 0.33$, d.f. $= 1$, $P > 0.05$). A regional breakdown suggests that OBIS is more complete than RIS where biodiversity monitoring is good, namely, around Europe, and the UK in particular, whereas RIS is better in the rest of the world (Table S3, available as Supplementary material to this paper).

Experts

Globally, 21 experts provided data for 99 Sites, of which 46 (47%) were reported to have bivalve reef and for the other 53 (54%) the absence of bivalve reef was reported. In no cases did the experts report no bivalve reef when the RIS had indicated the presence of bivalve reef. For a small number of Sites (six), experts provided contradicting reports. In these cases, it was assumed that false negatives are more likely than false positives and so the Sites were counted as having bivalve reefs. A regional breakdown is given in Table S4, available as Supplementary material to this paper.

Internet search

A total of 88 Sites was selected for internet searches from the 601 Sites with no prior evidence of a bivalve reef or reef-forming bivalve species. The searches found five Sites (6%) with evidence for bivalve reef and a further five (6%) with evidence for reef-forming bivalve species. A regional breakdown is given in Table S5, available as Supplementary material to this paper.

Discussion

The recent explicit recognition of bivalve-reef habitat within the wetland classification system of Ramsar Convention represents a significant acknowledgement of their ecological

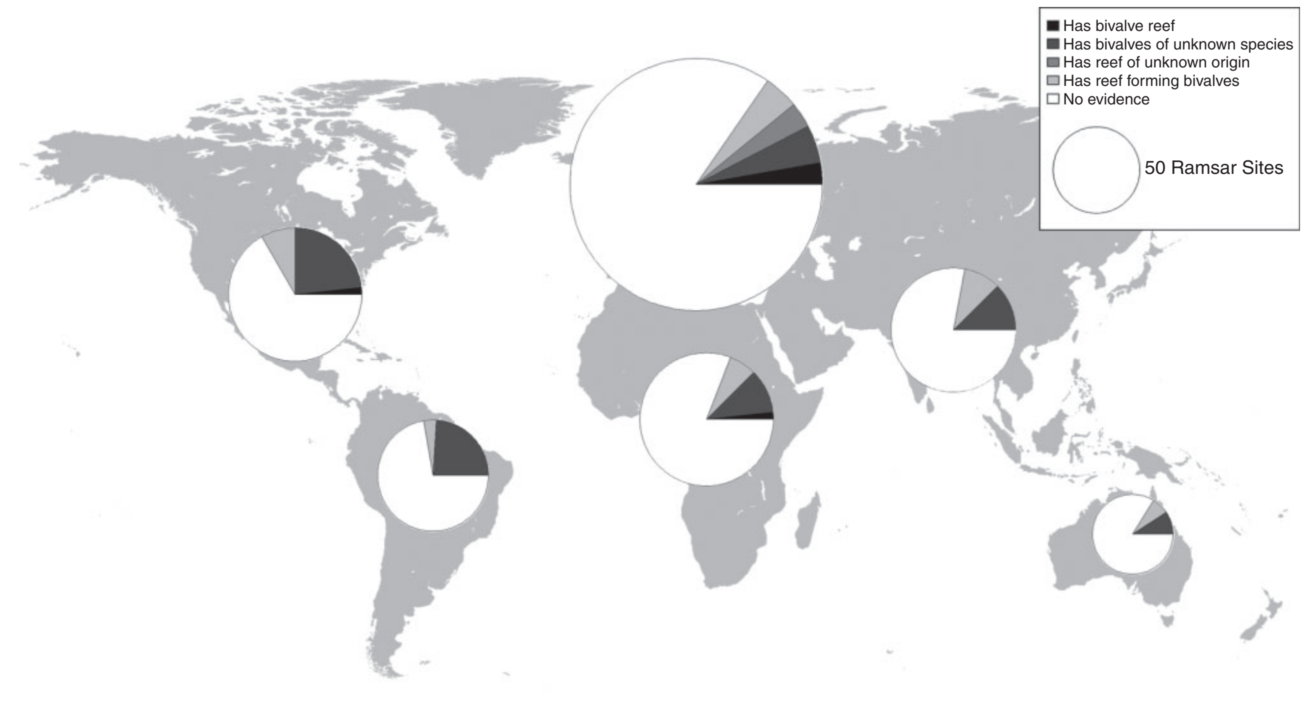

Fig. 1. Evidence for the presence of bivalve reef obtained from Information Sheet on Ramsar Wetlands (RIS), by region. Total area indicates the number of Ramsar study sites in each region. Map © WikiMedia Commons (by Crates, CC BY-SA 4.0-3.0-2.5-2.0-1.0, http://creativecommons.org/licenses/by-sa/4.0-3.0-2.5-2.0-1.0, from Wikimedia Commons).

and conservation importance. Our efforts here have illustrated that our knowledge of the location and extent of bivalve reefs is, however, limited. This data gap represents a significant challenge for the conservation of bivalve reefs, and for efforts of Ramsar Contracting Parties to update RISs for relevant Sites.

Using only RIS data would indicate that fewer than 2% of marine and coastal wetland Ramsar Sites have bivalve reefs, although a further 99 (11%) Sites had evidence of reef-forming bivalves. There was little evidence for a strong distinction between these two categories, with classification often depending on subtle details of the text.

Using alternative data sources (public databases, expert knowledge and general internet searches) demonstrated that the RIS documents frequently fail to report the presence of reef-forming bivalves and bivalve reef, although this is unsurprising because they were not required to do so. We also demonstrated that current biogeographic databases also vary in the completeness of their data, with a particular paucity of data from developing countries. In these regions, the RISs represent an important source of data, being one of the few mechanisms to capture and record biodiversity data in a standardised and widely available manner.

Our results seek to inform the ongoing process to ensure the accurate description and management of bivalve reefs within existing Ramsar Sites, as well as to identify potentially qualifying reefs that may qualify for Ramsar designation. Importantly, we have highlighted that bivalve reefs are often incompletely included on RIS descriptions of existing Sites and are, therefore, worthy of particular attention when updating the RIS by using current information sources. Novel surveys may be necessary to establish the status or even the presence of these often-subtidal habitats. To aid the process, we have highlighted some Sites where a bivalve reef is particularly likely to be present (given the presence of reef-building species) and so surveys are more likely to be fruitful (see Table S1). We highlight the importance of engaging with expert and local knowledge as a data source. We, furthermore, highlight again the scarcity of biological data for many of the less economically developed regions of the world and suggest that funding should be allocated so as to fill these data gaps.

Given that the current RISs do not require bivalves or bivalve habitat to be declared, it is notable that bivalves were mentioned in almost 20% of the Sites. This may reflect the value of bivalves to local communities; many of the remarks noted were in the context of bivalves being gathered (see Table S1), and harvested molluscs are important sources of protein, income and cultural heritage in many parts of the world (e.g. Siegfried *et al.* 1994; Dalzell *et al.* 1996; Kyle *et al.* 1997; Jimenez *et al.* 2011). Reef-building bivalves are, however, particularly susceptible to over-exploitation because their removal also degrades the biogenic reef habitat to which they recruit. Although recognition of their sensitivity and the need for exploitation to be sustainable has led to the protection of bivalves and other molluscs in some places (e.g. Bertocci *et al.* 2012; Alexander and Gladstone 2013), globally they remain at a significant risk (Beck *et al.* 2011).

The high level of reporting of harvestable species is a sharp contrast to the much lower level of reporting about bivalve reef as a habitat. This difference is likely to reflect a lack of knowledge of reef presence and a lack of awareness of the wider ecosystem benefits provided by the reef. Despite this, the number of Sites reported to have reef-forming bivalves should still give cause for optimism; although not all Sites with these species will have bivalve reef, a significant number are likely to. Furthermore, even if reef is not currently present, the presence of reef-forming species suggests that, with appropriate management, it might be possible to encourage reef formation in that Site or engage in active habitat restoration and, hence, enhance the Site quality. Such observations are important when considering the conservation of reef-building bivalves, as remaining habitat is often highly degraded (zu Ermgassen *et al.* 2012).

The lack of a single, globally comprehensive map of bivalve-reef habitat is a concern for their conservation (Guisan and Thuiller 2005, and references therein) and so effective reporting of its presence or absence in all Ramsar Sites around the world will be a major step towards resolving this issue. The present study used several different sources of information, and the necessity of this approach has been confirmed by the number of discrepancies among sources. Each method found a different, although overlapping, set of Sites to have reef-forming bivalves, demonstrating that none is complete. In the developed world, widespread biodiversity recording means that the RISs are a poor source of information relative to the various other biodiversity recording schemes; however, elsewhere, RISs are a much more significant contributor to biodiversity knowledge (Table S3), possibly because they concentrate scarce technical resources in small areas. In developing countries, poor integration of national recording with international initiatives contribute to the lack of available data (A. Carranza, pers. obs.). The widespread engagement of countries, non-governmental organisations and scientists with the implementation of the Ramsar Convention underpins the value of the Convention to improve biodiversity recording on a global scale. Expert knowledge is also important in developing countries (Table S4). Unlike the databases currently available, experts were often able to confirm the presence of bivalve reef itself, not just reef-forming species.

Whereas this work has focussed on reef-building bivalves, other bivalves can be important components of an ecosystem too, and therefore also deserve consideration and conservation. Infaunal bivalves, although not providing a structured habitat consistent with our proposed definition, can still strongly influence α diversity, water clarity and nutrient cycling (Smaal and Haas 1997; Coen *et al.* 2007). Some species of epifaunal bivalve, such as *Spondylus* spp., do not occur in sufficient densities to be considered a reef, but still act as a substrate for many other organisms (Mackensen *et al.* 2012). The presence of such bivalves not only dramatically increases the substrate surface area available to other organisms (Vicentuan-Cabaitan *et al.* 2014), but can also provide a valuable hard substrate when the sea bed is soft mud or sand. We note that before anthropic influences, densities may have been sufficient to qualify as reef. Furthermore, there remain biogenic reef-building species that are yet to receive attention (e.g. Vermetidae, Galil 2013) and we encourage recognition of these species too.

As a concluding remark, we would like to reiterate that, despite the ecological and economic importance of bivalve reefs, this habitat remains largely overlooked. The recent explicit recognition of bivalve reefs in the habitat classification of the Ramsar Convention is an important step forward in their conservation and in increasing the profile of this valuable habitat. We have demonstrated that the current RISs, unsurprisingly, are a poor reflection of the true likely extent of bivalve reefs within existing Ramsar Sites. These data provide us with an important baseline for monitoring progress in the reporting of this newly listed habitat type within the RIS. Our analysis of alternative data sources furthermore provides insight into Sites that may be worthy of closer examination during the revision of the RIS, as well as providing perspective on the value of available data sources. The strength of local and expert knowledge in Site-specific analysis cannot be understated. By highlighting the data gaps and opportunities presented by the Ramsar COP11, we seek here to contribute further to the conservation and understanding of bivalve-reef habitats.

Acknowledgements

This work was funded by The Nature Conservancy with support from the University of Cambridge. We thank all the contributors of data for the expert responses. We also thank Alexia Dufour and Nick Davidson of the Ramsar Secretariat for assistance in obtaining the RISs. Nick Davidson, David Stroud and two anonymous reviewers also provided valuable feedback on the manuscript.

References

Alexander, T. J., and Gladstone, W. (2013). Assessing the effectiveness of a long-standing rocky intertidal protected area and its contribution to the regional conservation of species, habitats and assemblages. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**, 111–123. doi:10.1002/AQC.2284

Baggett, L. P., Powers, S. P., Brumbaugh, R., Coen, L. D., DeAngelis, B., Greene, J., Hancock, B., and Morlock, S. (2014). 'Oyster Habitat Restoration. Monitoring and Assessment Handbook.' (The Nature Conservancy: Arlington, VA.)

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R. E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K., and Turner, R. K. (2002). Economic reasons for conserving wild nature. *Science* **297**, 950–953. doi:10.1126/SCIENCE.1073947

Beck, M. W., Brumbaugh, R. D., Airoldi, L., Carranza, A., Coen, L. D., Crawford, C., Defeo, O., Edgar, G. J., Hancock, B., Kay, M., Lenihan, H. S., Luckenbach, M. W., Toropova, C. L., and Zhang, G. (2009). 'Shellfish Reefs at Risk: a Global Analysis of Problems and Solutions.' (The Nature Conservancy: Arlington, VA.)

Beck, M. W., Brumbaugh, R. D., Airoldi, L., Carranza, A., Coen, L. D., Crawford, C., Defeo, O., Edgar, G. J., Hancock, B., Kay, M. C., Lenihan, H. S., Luckenbach, M. W., Toropova, C. L., Zhang, G., and Guo, X. (2011). Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* **61**, 107–116. doi:10.1525/BIO.2011.61.2.5

Bertocci, I., Dominguez, R., Freitas, C., and Sousa-Pinto, I. (2012). Patterns of variation of intertidal species of commercial interest in the Parque Litoral Norte (north Portugal) MPA: comparison with three reference shores. *Marine Environmental Research* **77**, 60–70. doi:10.1016/J.MARENVRES.2012.02.003

Borthagaray, A. I., and Carranza, A. (2007). Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. *Acta Oecologica* **31**, 243–250. doi:10.1016/J.ACTAO.2006.10.008

Carranza, A., Defeo, O., Beck, M., and Castilla, J. C. (2009). Linking fisheries management and conservation in bioengineering species: the case of South American mussels (Mytilidae). *Reviews in Fish Biology and Fisheries* **19**, 349–366. doi:10.1007/S11160-009-9108-3

Coen, L. D., Brumbaugh, R. D., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P., and Tolley, S. G. (2007). Ecosystem services related to oyster restoration. *Marine Ecology Progress Series* **341**, 303–307. doi:10.3354/MEPS341303

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., and van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260. doi:10.1038/387253A0

Dalzell, P., Adams, T. J. H., and Polunin, N. V. C. (1996). Coastal fisheries in the Pacific Islands. *Oceanography and Marine Biology: an Annual Review* **34**, 395–531.

DEFRA (2006). 'Ramsar Sites in England: a Policy Statement.' (Department for Environment, Food and Rural Affairs: London.)

Everitt, B. S. (1977). 'The Analysis of Contingency Tables.' (Chapman and Hall: London.)

Galil, B. S. (2013). Going going gone: the loss of a reef building gastropod (Mollusca: Caenogastropoda: Vermetidae) in the southeast Mediterranean Sea. *Zoology in the Middle East* **59**, 179–182. doi:10.1080/09397140.2013.810885

Gazeau, F., Quiblier, C., Jansen, J. M., Gattuso, J.-P., Middelburg, J. J., and Heip, C. H. R. (2007). Impact of elevated CO_2 on shellfish calcification. *Geophysical Research Letters* **34**, L07603. doi:10.1029/2006GL028554

Grabowski, J. H., Brumbaugh, R. D., Conrad, R. F., Keeler, A. G., Opaluch, J. J., Peterson, C. H., Piehler, M. F., Powers, S. P., and Smyth, A. R. (2012). Economic valuation of ecosystem services provided by oyster reefs. *Bioscience* **62**, 900–909. doi:10.1525/BIO.2012.62.10.10

Guisan, A., and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993–1009. doi:10.1111/J.1461-0248.2005.00792.X

Huber, M., and Gofas, S. (2013). Modiolarca Gray, 1847. (World Register of Marine Species.) Available at http://www.marinespecies.org/aphia.php?p=taxdetails&id=138221 [Verified 12 December 2013].

Jimenez, H., Dumas, P., Léopold, M., and Ferraris, J. (2011). Invertebrate harvesting on tropical urban areas: trends and impact on natural populations (New Caledonia, South Pacific). *Fisheries Research* **108**, 195–204. doi:10.1016/J.FISHRES.2010.12.021

JNCC (2006). UK Ramsar Sites. Available at http://jncc.defra.gov.uk/page-1389 [Verified 18 December 2013].

Kyle, R., Pearson, B., Fielding, P. J., Robertson, W. D., and Birnie, S. L. (1997). Subsistence shellfish harvesting in the Maputaland Marine Reserve in northern KwaZulu–Natal, South Africa: rocky shore organisms. *Biological Conservation* **82**, 183–192. doi:10.1016/S0006-3207(97)00022-0

Mackensen, A. K., Brey, T., Bock, C., and Luna, S. (2012). Spondylus crassisquama Lamarck, 1819 as a microecosystem and the effects of associated macrofauna on its shell integrity: isles of biodiversity or sleeping with the enemy? *Marine Biodiversity* **42**, 443–451. doi:10.1007/S12526-012-0120-9

Marencic, H., and de Vlas, J. (2009). Quality status report 2009 (25), Wadden Sea Ecosystem. Common Wadden Sea Secretariate, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.

NBN Trust (2013). NBN Gateway: Interactive Map Tool. Available at https://data.nbn.org.uk/imt/ [Verified 22 November 2013].

Newell, R. I. E. (2004). Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *Journal of Shellfish Research* **23**, 51–61.

Norling, P., and Kautsky, N. (2007). Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. *Marine Ecology Progress Series* **351**, 163–175. doi:10.3354/MEPS07033

OBIS (2013). Data from the Ocean Biogeographic Information System. (Intergovernmental Oceanographic Commission of UNESCO: Paris.) Available at http://www.iobis.org [Verified 2 December 2013].

Peterson, C. H., Grabowski, J. H., and Powers, S. P. (2003). Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Marine Ecology Progress Series* **264**, 249–264. doi:10.3354/MEPS264249

Prins, T. C., Smaal, A. C., and Dame, R. F. (1997). A review of the feedbacks between bivalve grazing and ecosystem processes. *Aquatic Ecology* **31**, 349–359. doi:10.1023/A:1009924624259

R Core Team (2014). R: a language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna.)

Convention, R. (1971). 'Convention on Wetlands of International Importance especially as Waterfowl Habitat. Ramsar, Iran, 2.2.1971as amended by the Protocol of 3.12.1982 and the Amendments of 28.5.1987' (Ramsar: Paris.) Available at http://www.ramsar.org/sites/default/files/documents/library/current_convention_text_e.pdf [Verified 10 February 2015].

Ramsar & Wetlands International (2013). 'Ramsar Sites Information Service.' Available at http://www.ramsar.wetlands.org/ [Verified 3 December 2013].

Romão, C., Reker, J., Richard, D., and Jones-Walters, L. (2012). 'Protected Areas in Europe: an Overview (5/2012).' (European Environment Agency: Copenhagen.)

Ruesink, J. L., Lenihan, H. S., Trimble, A. C., Heiman, K. W., Micheli, F., Byers, J. E., and Kay, M. C. (2005). Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology Evolution and Systematics* **36**, 643–689. doi:10.1146/ANNUREV.ECOLSYS.36.102003.152638

Scyphers, S. B., Powers, S. P., Heck, K. L., Jr, and Byron, D. (2011). Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. *PLoSONE* **6**, e22396. doi:10.1371/JOURNAL.PONE.0022396

Siegfried, W. R., Hockey, P. R., and Branch, G. M. (1994). The exploitation of intertidal and subtidal biotic resources of rocky shores in Chile and South Africa: an overview. In 'Rocky Shores: Exploitation in Chile and South Africa. Ecological Studies'. (Ed. P. D. W. R. Siegfried.) pp. 1–15. (Springer: Berlin.)

Smaal, A. C., and Haas, H. A. (1997). Seston dynamics and food availability on mussel and cockle beds. *Estuarine, Coastal and Shelf Science* **45**, 247–259. doi:10.1006/ECSS.1996.0176

Strategic Framework for the List (2009). 'Strategic Framework and Guidelines for the Future Development of the List of Wetlands of International Importance of the Convention on Wetlands (Ramsar, Iran, 1971).' Third edition, as adopted by Resolution VII.11 (COP7 1999) and amended by Resolutions VII.13 (1999), VIII.11 and VIII.33 (COP8 2002), IX.1 Annexes A and B (COP9 2005), and X.20 (COP10 2008)

Sutton, P. C., and Costanza, R. (2002). Global estimates of market and non-market values derived from nighttime satellite imagery, land cover, and ecosystem service valuation. *Ecological Economics* **41**, 509–527. doi:10.1016/S0921-8009(02)00097-6

The Council of the European Communities (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities. L* **206**, 7–50.

The European Parliament, The Council of the European Union (2009). Directive 2009/147/EC of the European Parliment and of the Council of 30 November 2009 on the conservation of wild birds (codified version). *Official Journal of the European Union. L* **20**, 7–25.

Vicentuan-Cabaitan, K., Neo, M. L., Eckman, W., Teo, S. L.-M., and Todd, P. A. (2014). Giant clam shells host a multitude of epibionts. *Bulletin of Marine Science* **90**, 795–796. doi:10.5343/BMS.2014.1010

zu Ermgassen, P. S. E., Spalding, M. D., Blake, B., Coen, L. D., Dumbauld, B., Geiger, S., Grabowski, J. H., Grizzle, R., Luckenbach, M., McGraw, K., Rodney, W., Ruesink, J. L., Powers, S. P., and Brumbaugh, R. (2012). Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. *Proceedings. Biological Sciences* **279**, 3393–3400. doi:10.1098/RSPB.2012.0313