

Sydney Harbour: what we do and do not know about a highly diverse estuary

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Abstract. Sydney Harbour is a global hotspot for marine and estuarine diversity. Despite its social, economic and biological value, the available knowledge has not previously been reviewed or synthesised. We systematically reviewed the published literature and consulted experts to establish our current understanding of the Harbour's natural systems, identify knowledge gaps, and compare Sydney Harbour to other major estuaries worldwide. Of the 110 studies in our review, 81 focussed on ecology or biology, six on the chemistry, 10 on geology and 11 on oceanography. Subtidal rocky reef habitats were the most studied, with a focus on habitat forming macroalgae. In total 586 fish species have been recorded from the Harbour, which is high relative to other major estuaries worldwide. There has been a lack of process studies, and an almost complete absence of substantial time series that constrains our capacity to identify trends, environmental thresholds or major drivers of biotic interactions. We also highlight a lack of knowledge on the ecological functioning of Sydney Harbour, including studies on microbial communities. A sound understanding of the complexity, connectivity and dynamics underlying ecosystem functioning will allow further advances in management for the Harbour and for similarly modified estuaries around the world.

Additional keywords: Australia, biodiversity, harbours, Port Jackson, urbanisation.

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Introduction

Sydney Harbour is an estuary at the heart of Australia's largest city and a hotspot for biological diversity. Despite the economic,

social and ecological importance of Sydney Harbour, there are no published syntheses of the biophysical literature regarding the Harbour. Understanding the biophysical nature of a location

is a crucial step towards determining the ecological constraints within natural systems and identifying preventive and remedial measures to ensure sustainable and effective management (Christensen *et al.* 1996). It is also a rigorous way to pinpoint critical knowledge gaps. Other major estuaries have benefited significantly from such holistic reviews (e.g. Chesapeake Bay, USA; Orth and Moore 1984; Kemp *et al.* 2005; and Victoria Harbour, Hong Kong; Yung *et al.* 1999). This review of our current understanding of Sydney Harbour, and the identification of knowledge gaps, will assist in planning research and management actions for the Harbour and can inform similar practices for estuaries around the world.

Estuaries are among the most diverse and productive ecosystems in the world, hosting an array of habitats and providing essential goods and services to society such as trade opportunities, recreational amenities and seafood (Costanza *et al.* 1997, 2014). Sydney Harbour is no exception; the Harbour includes a wide variety of habitats and organisms supporting biological diversity that is rarely matched in other estuaries within Australia or worldwide (Hutchings *et al.* 2013). The Harbour plays a pivotal role in the life of Sydney-siders for aesthetic and ecological reasons, and also due to its socioeconomic importance – it is heavily used for tourism and recreational activities such as fishing, swimming, sailing, diving, and cruises (Hedge *et al.* 2014).

Both the beauty and the biodiversity of Sydney Harbour appear to be strongly supported by the large size and the special geological structure of the Harbour. The Harbour, one of the largest estuaries in the world, is a drowned river valley with a wide, open mouth. Drowned river valleys are characterised by rocky walls that retain relatively little sediment at the entrance and a series of complex shallow embayments with high sediment and water retention times in the upper reaches. This complex structure is able to host a wide variety of habitats (Roy *et al.* 2001). In Sydney Harbour these habitats support a great diversity of organisms rarely found in other estuary types or even coastal systems (Roy *et al.* 2001; Clynick and Chapman 2002; Chapman 2006; Clynick 2008a, 2008b; Creese *et al.* 2009). A total of 2473 species of polychaetes, crustaceans, echinoderms and molluscs have been recorded from the Harbour (Hutchings *et al.* 2013). By comparison, 1636 species have been recorded from neighbouring Botany Bay, 981 from Port Hacking (Fraser *et al.* 2006), and 1335 from the Hawkesbury River (Hutchings and Murray 1984). In the entire Mediterranean Sea, only 5678 species of polychaetes, crustaceans, echinoderms and molluscs have been recorded (Coll *et al.* 2010). Moreover, Mediterranean records represent centuries of sample collection, greater taxonomic expertise, and a much greater collection area (2 500 000 km² compared with Sydney's 55 km²). The number of fish species recorded for Sydney Harbour (586) (Booth 2010; Hutchings *et al.* 2013) is also extremely high when compared with other harbours or bays worldwide such as Chesapeake Bay, USA (207), Puget Sound, USA (155) and San Pedro Bay, Philippines (155; see FishBase, <http://www.fishbase.org>, accessed 7 September 2015).

Understanding interactions between biological and physico-chemical properties of an ecosystem can help us predict patterns of diversity and abundance and should guide the development of effective policies for management and conservation. Assessing interactions also provides additional information about the

processes constraining and defining subtropical–temperate estuarine environments. Sydney Harbour is subjected to several anthropogenic stressors that threaten its biological resources and, consequently, its commercial and recreational value. Before assessing threats, however, it is important to understand the Harbour's biophysical structure and dynamics. This paper reviews our current understanding of the geology, hydrology, chemistry and ecology of Sydney Harbour. Despite the iconic nature of this estuary, there have been no previous compilations of the scientific knowledge or identification of knowledge gaps for Sydney Harbour. In comparison, comprehensive surveys or reviews have been undertaken for other estuaries in Australia (e.g. Port Phillip Bay and Moreton Bay; Stephenson *et al.* 1970; Wilson *et al.* 1998; Hewitt *et al.* 2004; Pantus and Dennison 2005) and the world (e.g. Chesapeake Bay, USA; Orth and Moore 1984; Kemp *et al.* 2005; and Victoria Harbour, Hong Kong; Yung *et al.* 1999). A follow-up companion paper, by the same authors, reviews our understanding of human impacts within this heavily modified estuary (Mayer-Pinto *et al.* 2015).

We collated information regarding the geology, hydrology, chemistry and ecology of Sydney Harbour, using four search methods – systematic online literature searches, interviews, surveys and a workshop with experts. The information we uncovered was then analysed and synthesised to create a comprehensive review of natural systems within the estuary and to identify knowledge gaps. Finally, on the basis of our review, we propose directions for future research.

Literature review

Our review used four search methods: (1) a systematic literature search of databases, using the keywords: 'Sydney Harbour' or 'Sydney Harbor', and 'Port Jackson' or 'Parramatta River'; (2) a questionnaire, distributed to 111 scientists from around the world who have used the facilities at the Sydney Institute of Marine Science; (3) direct approaches to Sydney-based research groups, and (4) a 2-day workshop and discussion with an interdisciplinary panel of marine scientists. Workshop participants examined literature relating to their particular fields of expertise and highlighted works missing from our initial search. This allowed relatively obscure yet important texts to be included, as well as highlighting many unpublished works not available on searchable databases. This was a key component of our search methods, as many important texts failed to include 'Sydney Harbour' or similar search terms in either the article title or its keyword list.

The titles and abstracts of each of the articles and reports identified were examined; those mentioning the natural habitats (e.g. mangroves, rocky reefs, open water) or biophysical processes of the Harbour, including its geology and chemistry, were included in the review. Sydney Harbour is an inlet on the east coast of Australia (Tasman Sea, South Pacific). The entrance between North and South Heads is ~33°50'S, 151°17'E. The Harbour was defined to include all of the Parramatta River, Lane Cove and Middle Harbour (Fig. 1). This included papers and reports with data collected from locations up to 1 km along the coastline north and south of the Sydney Harbour entrance. Where possible, articles were assigned to a Field of Study (e.g. Ecology, Oceanography), and a Habitat Type (e.g. rocky intertidal, open

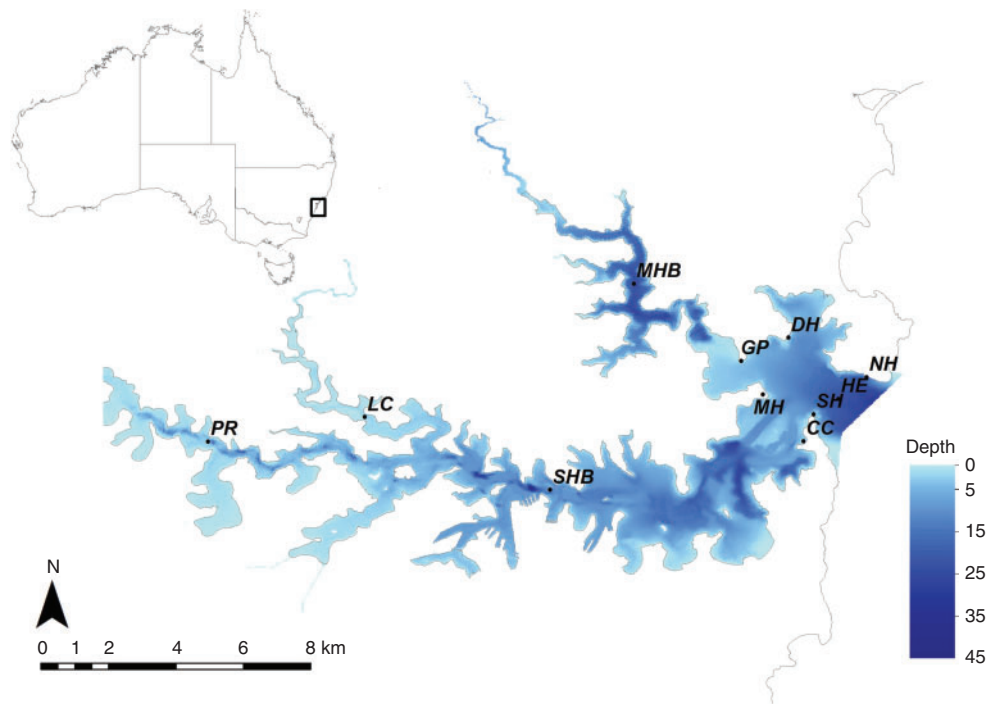


Fig. 1. Map of the Sydney Harbour, detailing its bathymetry and some geographical points (mentioned in the text). CC, Camp Cove; DH, Dobroyd Head; GP, Grotto Point; HE, Harbour Entrance; LC, Lane Cove; MH, Middle Harbour; NH, North Head; PR, Parramatta River; SH, South Head; SHB, Sydney Harbour Bridge.

water). Articles with no clear habitat focus were not assigned a habitat term (e.g. management-related articles). All studies considered fundamental research or independent of an anthropogenic threat were included in this review.

Results of the literature review

Overview

Of the 310 journal articles and reports identified in our search, 110 focussed on natural history and science and were included in this review (see Supplementary material). Human impact studies were included only where necessary to give a full understanding of biophysical aspects of the Harbour – this is because a second review analysing the studies of human impacts in Sydney Harbour has been prepared separately (Mayer-Pinto *et al.* 2015). Of the 110 studies included here, 81 focus on the ecology or biology of Sydney Harbour, in comparison to only six reporting on the chemistry of the Harbour, 10 on the geology and 11 on oceanographic processes.

Of the biological studies, the natural history of subtidal rocky reefs was the most commonly studied (~36%), followed by mangroves and saltmarshes (~15%), and intertidal rocky shores, seagrass and open water (<10% each). Less than 1% investigated the Harbour's sandy intertidal environments (Fig. 2; Dexter 1983a, 1983b; Keats 1997).

Physico-chemical characteristics of Sydney Harbour

Geological history

Several processes contribute to the formation of estuaries including climatic factors, sea level changes and tides and these

operate within a geologic framework (Eliot and Eliot 2008). There are over 1000 estuaries in Australia, and most formed due to rising sea levels following the last ice age, some 6000 to 15 000 years ago (Kench 1999). Estuaries can be generally classified into five groups: (1) bays; (2) tide-dominated estuaries; (3) wave-dominated estuaries; (4) intermittent estuaries and (5) freshwater bodies, and there are different types of estuaries within each of these groups (Roy *et al.* 2001). For example, the Sydney estuary is a tide-dominated estuary, and more specifically a drowned river valley – a relatively common type of estuary in southern Australia. The bedrock of Sydney estuary dates to the Permian to Triassic age (300–220 million years) Sydney Basin and is dissected up to 85 m into Hawkesbury Sandstone and overlying Ashfield Shale (Roy 1981). The configuration of the Sydney estuary catchment drainage system and the orientation of bays and shorelines are controlled by the faults and fractures within its geological structure. The Parramatta River, which eroded the current Sydney estuary, may once have been connected to the Nepean River, which may later have been 'captured' by the Hawkesbury River between 15 and 29 mya (authors unpubl.). During periods of uplift, the river eroded into bedrock forming steep-sided banks, whereas during interglacial periods, sea level rose and the 'river' was flooded, leaving deep deposited sediments in the estuary.

During the Quaternary period (~2.5 million years ago to the present) there have been sea level oscillations every 100 000 to 150 000 years as a result of global climate change and glaciation. For the majority of the last 135 000 years, the global sea level was between 20 and 70 m below the current level, suggesting that erosion processes were more pronounced than

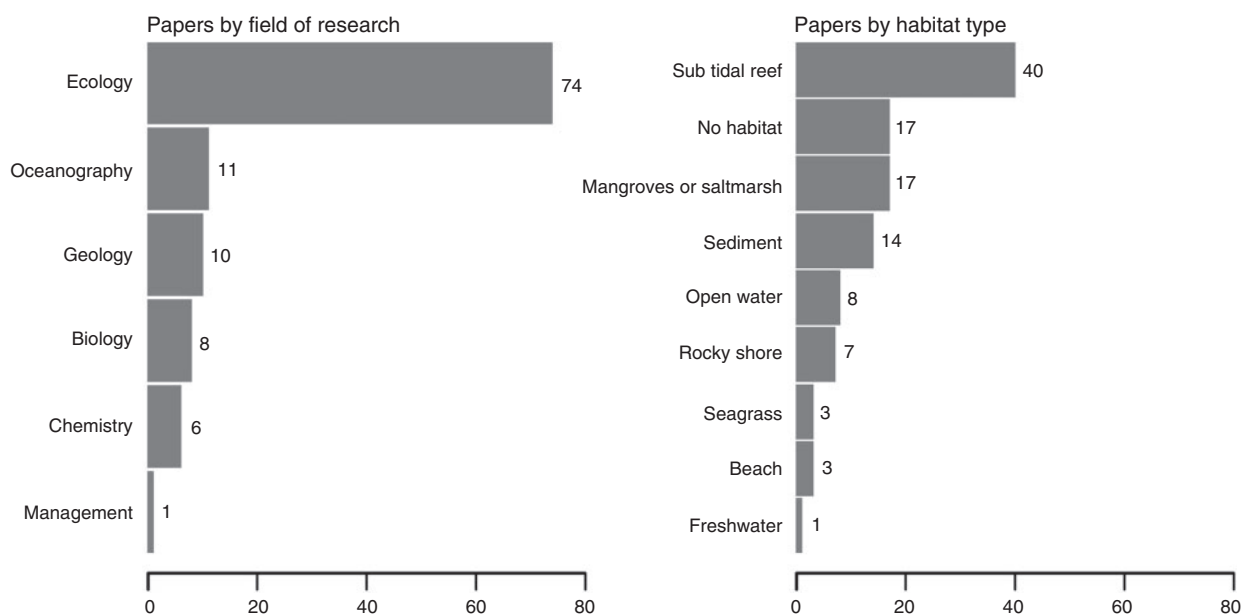


Fig. 2. Number of studies that have assessed the biophysical aspects of Sydney Harbour, separated by field of research and types of habitats.

deposition processes (Roy 1981). The last glacial period ended c. 17 000 years ago and the sea level rose quickly. By 10 000 years ago, sea levels had increased from ~100 m below current levels to 25 m below current levels. As a result the water's edge moved from 25 to 30 km east of its present position to 3–5 km off the present day coastline. The sea advanced into the Sydney river valley, forming a flood-tide delta. Sediment was deposited by rivers in the upper parts of the estuary as fluvial deltas.

Hydrography

The poleward flowing East Australian Current (EAC) and its eddy field off the coast of Sydney provides a nutrient depleted subtropical water mass on the continental shelf adjacent to the Harbour's entrance (Roughan and Middleton 2002, 2004). This is consistent with the fact that the EAC is a western boundary current and these are considered low in nutrients worldwide. Current speeds offshore can be up to 1.5 m s^{-1} in as little as 65 m of water (Middleton *et al.* 1997), and water flowing past the entrance to the Harbour is continually being renewed. Ten km offshore – at the 100 m isobath – oceanic temperatures range between 12 and 25°C in February. Temperatures are generally more mixed in winter ranging between 16 and 20°C in June, with salinity ranging from 35.2 to 35.6 psu (M. Roughan, unpubl. data). The colder bottom waters during summer are typically the result of wind- and current-driven upwelling and are high in nutrient concentrations (Schaeffer *et al.* 2013). This upwelled water is a potential source of nutrient enrichment in the estuary. Monthly average surface sea temperatures in Sydney Harbour vary from 24°C in summer to 15°C in winter (Bureau of Meteorology website, accessed 15 January 2015).

The bathymetry of Sydney Harbour is complex, with an average depth of 13 m, including channels for shipping varying from ~28 to 45 m and shoals with depths of 3–5 m (Fig. 1). This

complex bathymetry makes Sydney Harbour one of the few harbours worldwide that does not require maintenance dredging, unlike San Francisco Bay and Victoria Harbour in Hong Kong, for instance. The estuary consists of several large, shallow bays adjacent to the main channel, which represent a large reservoir for tidal waters and potential pockets of water with higher residence time than the main channel. The present day estuary comprises five environmental or sedimentological units: the entrance (marine flood-tide delta sands), lower estuary (sands), central estuary (muddy sands) and upper estuary (muds) and the off-channel embayments (muds).

Salinity concentration in Sydney Harbour is mainly driven by the balance between the restricted freshwater inflow from the catchments running to the estuary (mainly Parramatta, Lane Cove and Middle Harbour), precipitation and evaporation. Land runoff and several small creeks that flow into the Harbour during rain events also influence the salinity in the Harbour. The rainfall pattern in Sydney is erratic and strongly influenced by El Niño–La Niña weather cycles. For instance, average mean monthly rainfall ranged from a minimum of 69.1 mm in September to a maximum of 130.6 mm in June between the years 1859 and 2010 (Lee *et al.* 2011). Nevertheless, the Sydney catchment can be characterised as having dry conditions, punctuated by infrequent, high precipitation events (rainfall $>50 \text{ mm day}^{-1}$). During dry weather (rainfall $<5 \text{ mm day}^{-1}$), which constitutes the majority of the year, the estuary is well mixed (normal ocean salinity) with only a small quantity of freshwater entering Sydney Harbour, making this an almost marine estuary (Birch 2007; Birch and Rochford 2010). After strong rains, however, salinity can drop considerably in the top 4 m of the water column, causing some stratification. These conditions are unusual for estuaries in general, which are typically more mixed with fresh and saline water (Birch 2007).

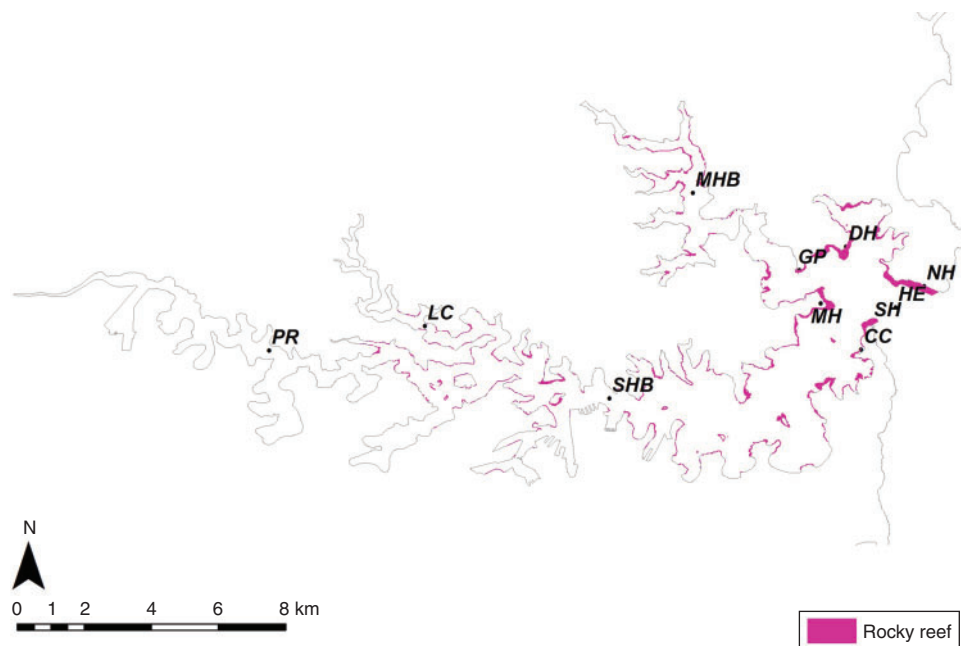


Fig. 3. Map of the distribution of the subtidal rocky reefs habitats in Sydney Harbour and some geographical points (mentioned in the text). CC, Camp Cove; DH, Dobroyd Head; GP, Grotto Point; HE, Harbour Entrance; LC, Lane Cove; MH, Middle Harbour; NH, North Head; PR, Parramatta River; SH, South Head; SHB, Sydney Harbour Bridge.

Circulation

Circulation within Sydney Harbour is tidally dominated, with some influence from prevailing winds. Sydney estuary is a micro-tidal system with a range of 2.1 m. Tidal forcing is predominantly semi-diurnal with amplitude $M2 = 0.501$ m, $S2 = 0.126$ m, $K1 = 0.148$ m and $O1 = 0.096$ m (Das *et al.* 2000). Tidal velocities are periodic, reversing every 6 h and varying considerably in magnitude both spatially and over a tidal period. Towards the mouth of the Harbour, depth averaged tidal velocities typically range from 0.1 to 0.25 m s⁻¹ over the spring neap cycle (in 15 m of water, M. Roughan, unpubl. data). In the furthest branches of the estuary, both modelling and observations reveal velocities an order of magnitude lower (Das *et al.* 2000).

During spring tides, the ebb flow from the Harbour is strongest near the northern side of the entrance and a clockwise eddy is formed (Middleton *et al.* 1997). Repeat velocity transects across the mouth show some vertical velocity variation, with inflow on the southern side. Maximum velocities are ~ 0.25 m s⁻¹ in the surface waters at the mouth of the Harbour (M. Roughan, unpubl. data).

Circulation patterns vary depending on the wind direction, which contributes to differences in retention of oceanic waters and rates of flushing. Das *et al.* (2000) estimated discharge volumes to be up to 6000 m³ s⁻¹ across the heads, at the peak of the ebb tide, with more than 4000 m³ s⁻¹ coming from the main branch of Port Jackson (including the Parramatta and Lane Cove Rivers) and less than 1500 m³ s⁻¹ coming from Middle Harbour. Flushing rates range from few days to up to 225 days for embayments near the headwaters. So, despite the large flushing

in the entrance of the estuary – probably due to the large and deep opening of the heads – flushing is generally poor in the Harbour overall, especially in the upper estuary (Das *et al.* 2000). Offshore surveys reveal that even under dry conditions, tidal outflows from Sydney Harbour can extend several kilometres offshore (Middleton *et al.* 1997).

The natural habitats of Sydney Harbour

Subtidal rocky reefs

Subtidal reefs defined by Witman and Dayton (2001) as ‘any benthic habitat composed of hard substrate from the intertidal–subtidal fringe down to the upper limit of deep sea’ are among the most diverse and productive environments in the world (Mann and Breen 1972; Steneck *et al.* 2002). Subtidal rocky reefs occur throughout the Harbour, but have only been mapped at selected sites – Grotto Point, Dobroyd Head and Middle Head (Fig. 3). These sites constitute ~ 1.58 km² of reef and are dominated by macroalgae (38%), with an additional mix of macroalgae and barrens (25%), barrens (18%), sessile invertebrates (8%), turfing algae (5%) and a mix of macro and turfing algae (5%) (Fig. 3) (Creese *et al.* 2009).

Kelps (macroalgae of the Order Laminariales) are usually the dominant habitat forming organisms in temperate shallow subtidal reefs around the world (Steneck *et al.* 2002) and this is also true for Sydney Harbour. This dominance of a native kelp (*Ecklonia radiata*) seems to be a distinctive feature of the Harbour in comparison to other urbanised temperate estuaries around the world, e.g. San Francisco Bay, where introduced species of macroalgae such as *Sargassum muticum* and *Codium*

fragile are common and abundant (Josselyn and West 1985). A consequence of the presence of these kelp beds is the great biological diversity that occurs in and around subtidal reefs in this estuary. Kelp systems are extremely productive and their growth depends on interactions between temperature, nutrient availability and light (Steneck *et al.* 2002). A study at one site in Sydney Harbour – Fairlight Bay – in the early 1980s, estimated the annual mean kelp productivity to be $2.9 \text{ kg DW m}^{-2} \text{ year}^{-1}$ (Larkum 1986). This represents an annual mean of $790 \text{ g C m}^{-2} \text{ year}^{-1}$, which is within the range found for other kelps around the world (Larkum 1986).

Most studies of subtidal reefs in Sydney Harbour have concentrated on *E. radiata* and *Sargassum* spp., the dominant habitat forming algae in Sydney Harbour, and the organisms they support. Beds of *Ecklonia* inside the Harbour support a variety of important mobile and sessile epibiota, such as dwelling sea-urchin *Holopneustes purpurascens* and several species of bryozoans, sponges, hydroids and filamentous algae (For a complete list of the species present in these habitats see Fletcher and Day 1983; Kennelly 1987b; Steinberg 1995; Connell and Glasby 1999; Glasby 1999; Clynick *et al.* 2008; Marzinelli *et al.* 2011). *Sargassum* spp. beds in the Harbour also support diverse assemblages of organisms, particularly isopods and amphipods (Poore and Lowry 1997; Poore and Hill 2005).

Some of the key ecological processes acting on the subtidal reef communities inside the Harbour include grazing, recruitment, competition and natural disturbances such as storms, which influence the composition and relative abundance of understory assemblages in *Ecklonia* beds (Kennelly 1987a, 1987b). Storms can dislodge the kelp creating clearings within the bed and this leads to a decrease in abundance of encrusting algae, sponges and colonial ascidians and an increase in cover of turfing algae (Kennelly 1987b). Fish activity also modifies understory species in *Ecklonia* beds in the Harbour such as *Giffordia mitchelliae*. The experimental exclusion of carnivorous fish (e.g. *Upeichthys lineatus*) in *Ecklonia* beds led to an increase in the abundance of small invertebrate grazers, which caused reduced understory algal growth (Kennelly 1991). On the open coast of Sydney, urchins and limpets maintain most of the substratum covered by encrusting coralline algae (>80%) and keep covers of foliose algae low (<10%) (Fletcher 1987; Andrew and Underwood 1989; Andrew 1993). However, no studies have examined the effects of urchins on kelp beds in the Harbour.

Very few studies have focussed on other subtidal reef habitats in the Harbour. Coleman (2002) investigated intertidal and subtidal turfing algal communities at one location in the Harbour (Camp Cove). These communities varied in composition and relative abundances at very small spatial scales (tens of centimetres), suggesting that small scale processes influence patterns of distribution and abundance of these subtidal turfs in the estuary (Coleman 2002). There are also several deep water reefs (>20 m) in the Harbour, supporting diverse assemblages of sponges, as well as ascidians, bryozoans and cnidarians (Roberts *et al.* 2006). Processes operating at smaller scales appear to shape these assemblages (Roberts *et al.* 2006).

The most speciose fish families inhabiting subtidal rocky reefs of Sydney Harbour are Labridae (wrasses), Gobiidae (gobies) and Pomacentridae (damselfishes), with 45, 32 and 26 species respectively. It is important to note that Sydney is a

globally high diversity region for syngnathids (seahorses and their allies: 19 species found in Sydney). Furthermore, several species of fishes are endemic to Sydney subtidal habitats, including the Sydney Scorpionfish *Scorpaenopsis insperatus* Motomura, discovered in Chowder Bay, outer Sydney Harbour, in 2004, and Sydney's Pygmy Pipehorse *Idiotropiscis lummitzeri* Kuiter, discovered in 2004 and known only from Sydney coastal waters (Booth 2010).

Rocky reefs in the greater Sydney region have been surveyed for fish and mobile invertebrate diversity and abundance in an *ad hoc* manner since 2008 as part of the Reef Life Survey citizen science project. A recent publication from this work (Stuart-Smith *et al.* 2015) has shown the relatively high fish diversity of Sydney Harbour (20–25 species per 500 m²) compared with other heavily urbanised estuaries in Australia (Port Phillip Bay and Derwent Estuary with 5–10 species per 500 m² each). This study also indicated that within Sydney Harbour, heavily impacted sites (as characterised by (Birch and Taylor 1999) had fewer fish and invertebrates, reduced total fish biomass and tended to be characterised by smaller fish species.

Rocky intertidal shores

Rocky shores occur throughout the coastlines of oceans, laying between the low and high water marks that fringe entire countries, coasts and estuaries (Crowe *et al.* 2000; Menge and Branch 2001). This already large habitat is further increased by the addition of a myriad of artificial structures increasingly added to coastal shores, such as seawalls and groynes (Crowe *et al.* 2000), which usually harbour many species found on the natural shores.

In Sydney Harbour, intertidal shores are usually horizontal or gently sloped sandstone platforms (Bulleri *et al.* 2005; Cole 2009; Cole *et al.* 2005). They have little exposure to waves and a tidal range of ~1.5 m (Cole 2009). There are, however, some completely vertical natural rocky shores ~15–20 m long (e.g. Chapman 2003a; Bulleri 2005b; Bulleri *et al.* 2005). Boulder fields also comprise some of the intertidal rocky habitats in the Harbour and, although they are not particularly common, they support a great diversity of organisms living on, or under, the boulders (Chapman 2002, 2003b).

Chapman (2003a), in a study of intertidal sea walls and natural shores at three sites east of the Harbour bridge, found a total of 127 taxa (predominantly molluscs), including sessile and mobile species, dispersed along the shoreline. There was great spatial variability in the diversity of species at different heights of the shore and between sites. Generally, however, the low intertidal area of Sydney Harbour is dominated by foliose algae, the tubiculous calcareous polychaete *Galeolaria gemineoa* or the ascidian *Pyura praeputialis*, whereas the mid-shore assemblages are dominated by the presence of the Sydney Rock Oyster *Saccostrea glomerata*, limpets, barnacles and encrusting algae (Chapman 2003a; Goodsell 2009). For a list of the species found on natural shores in the Harbour, see Bulleri (2005a). Some species form important biogenic habitats such as oyster, worm or algal beds that support a high diversity of associated organisms (Coleman 2002; Cole *et al.* 2007; Cole 2009; Matias *et al.* 2010). The distribution of these habitat forming organisms on intertidal shores in Sydney is naturally patchy, forming mosaics on and around the shoreline (Cole *et al.* 2007).

Naturally occurring rocky shores in Sydney Harbour are, however, extremely fragmented (Goodsell *et al.* 2007; Goodsell 2009), with most of the natural coast replaced by seawalls (Chapman and Bulleri 2003). Habitat fragmentation and the replacement of natural shores by built structures negatively affects intertidal communities in the Harbour and are discussed in detail in our companion study of human impacts in Sydney Harbour (Mayer-Pinto *et al.* 2015).

Soft bottoms and beaches fauna

Marine sediments cover over 80% of the ocean floor and their communities provide important ecosystem services such as nutrient recycling (Lenihan and Micheli 2001). Biota associated with soft sediment habitats ranges from bacteria to benthic feeding whales and represent important trophic links in coastal and estuarine systems. The composition of these communities varies according to sediment size, type and organic content. These parameters are, in turn, controlled by abiotic factors such as current strength, wave activity and successional processes after disturbance (Lenihan and Micheli 2001). Most sediment infauna can be found within the surface few centimetres (Hutchings 1998; Lenihan and Micheli 2001). Infaunal organisms often act as bio-turbators, having profound effects on sediment nutrient cycling, oxygenation, water content, porosity and chemical make-up (Kogure and Wada 2005).

Soft sediment habitats are important in the functioning of systems and critical for many of the fish and crustaceans including important recreational species (e.g. Freckman *et al.* 1997; Snelgrove *et al.* 1997). Despite the importance of these habitats and their biota in general, no comprehensive taxonomic surveys of soft bottom benthic communities of Sydney Harbour have been undertaken. Some intertidal samples in mud flats around Homebush Bay were collected as part of a bird feeding survey (Hutchings 1996) and subtidal benthic communities were sampled by grabs as part of a survey done by the Australian Museum to detect invasive marine pests in the Harbour (AM 2002). These data are included in Hutchings *et al.* (2013).

Although only four natural history studies have investigated intertidal infaunal communities at Sydney Harbour (Dexter 1983a, 1983b; Keats 1997; Jones 2003), there have been several studies of soft sedimentary environments in relation to contamination (e.g. Birch *et al.* 1999, 2008; Birch and Taylor 2000; McCready *et al.* 2006; Birch and Rochford 2010; Dafforn *et al.* 2012, 2013). Dafforn *et al.* (2013) found Sydney Harbour to be one of the most diverse harbours along the coast of NSW for infaunal organisms, especially polychaetes, despite high levels of contaminants in the sediments. The authors also found that polychaetes comprised up to 75% of the sediment's macrofauna, with great abundances of individuals from the families Arabelidae, Spionidae, Nephytidae, Cirratulidae, Maldanidae and Capitellidae.

The microbiota in soft sediments have a central role in the functioning of ecosystems as they form the basal elements of many food chains, affect sediment chemistry and restrict nutrient availability (Gadd and Griffiths 1977). Therefore, a comprehensive understanding of sediment microbial community is extremely important for understanding and managing these natural systems. A study quantifying the bacterial communities

of sediments within the Harbour found 4640 Operational Taxonomic Units (OTUs) (Sun *et al.* 2012). This is likely to be a conservative estimate as Sun *et al.* (2012) used 454 Pyrosequencing of the 16S and 23S rRNA genes, where debate exists as to the interpretation of 'rare' sequences. Chariton *et al.* (2010), sequenced the 18S rDNA also using the 454 Pyrosequencing, found 10 091 different OTUs from 262 Orders, 122 Classes and 54 Phyla in a smaller scale study at two other sites within the Harbour: the Lane Cove and Parramatta River. Note that this estimate of diversity included metazoans (such as Bivalves and Polychaetes) as well as microzoans (e.g. Ascomycota and Bacillariophyceae). Both studies give an indication of the great diversity of organisms living in soft sedimentary environments in Sydney Harbour and suggest further research is warranted in order to truly describe the diversity of this habitat.

Soft sediment macrophytes

Seagrass, mangroves and saltmarshes are highly productive and are habitat for a variety of organisms, including some economically important (e.g. Field *et al.* 1998; Duarte 2002; Orth *et al.* 2006; Wilson and Koutsagiannopolou 2014). In addition, such systems reduce erosion, providing natural protection for the coastal zone against storms and waves (e.g. Orth *et al.* 2006; Foster *et al.* 2013).

Seagrasses, mangroves and saltmarshes have significant differences regarding their taxonomy and ecology; comprise different habitats and contribute differently to the functioning of the Sydney estuary. The term mangrove refers to a group of ~55 species of phylogenetically unrelated plants that have adaptations to allow for living in high salinity environments (Tomlinson 1986). Mangroves form extensive forest systems along the intertidal areas throughout the tropical and warm temperate world, usually between 25°N and 25°S where water temperatures do not usually fall below 20°C during winter (Connolly and Lee 2007).

Two species of mangroves occur in Sydney Harbour: the grey mangrove, *Avicennia marina*; and the river mangrove, *Aegiceras corniculatum* (Creese *et al.* 2009) and the litter material from these trees forms the basis of detrital food webs that support a variety of species at most trophic levels (e.g. algae, barnacles, molluscs, fish; Ross and Underwood 1997; Chapman 1998; Ross 2001; Chapman *et al.* 2005; Tolhurst 2009). In addition, many species of macroalgae are found on mangrove pneumatophores and these epiphytic algae may be useful indicators of contamination in the Harbour (Melville and Pulkownik 2006, 2007).

A large number of halophytic species are contained within the group collectively known as 'saltmarsh' and, in 2004, the NSW Scientific Committee identified 10 species of saltmarsh plants in the Sydney Metropolitan area (see complete list of species in Kelleway *et al.* 2007). Saltmarshes provide several important ecosystem services such as coastal protection and filtering of sediments and nutrients (Pennings and Bertness 2001). Unlike saltmarshes in the US and Europe, saltmarshes in Australia exist in the zone immediately above mangrove forests along sheltered estuarine shorelines (Adam 1990). Although mangroves are predominantly tropical in their distribution, saltmarshes are primarily temperate. In Australia,

however, it is interesting to note that saltmarsh area is generally greater in estuaries along the tropical Queensland coast (Connolly and Lee 2007).

Seagrasses are the only estuarine plants that can live totally submerged in oceanic water and they form some of the most productive systems in the world. Seagrass meadows support important commercial fisheries around the globe and provide essential services such as sediment stabilisation, sequestration of carbon and nutrient cycling (Orth *et al.* 2006). Three species of seagrasses occur in Sydney Harbour: *Halophila ovalis*, *Zostera capricornis* and *Posidonia australis* (Widmer 2006), which is considered a relative low diversity, compared with other parts of Australia and the globe (Short *et al.* 2007). South-western Australia, for instance, is considered one of the most diverse areas of the world, with more than 10 temperate and tropical species of seagrasses (Short *et al.* 2007). Despite the importance of seagrass habitats, little is known about these within the Harbour.

Aerial photographs have been used to map estuarine macrophytes for NSW estuaries including Sydney Harbour (Fig. 4) (Creese *et al.* 2009). The spatial extent of saltmarsh in Sydney Harbour has declined significantly since colonisation (McLoughlin 2000; West *et al.* 2004; West and Williams 2008). Extensive mudflats and saltmarsh communities appear to have dominated the intertidal zone of the Harbour in the 19th century (McLoughlin 2000), whereas, in 2005, the area mapped from aerial photographs was less than 37 ha (Kelleway *et al.* 2007). It is difficult, however, to identify small patches from aerial photographs, so the extent is probably slightly underestimated. The largest contiguous patch of saltmarsh remaining in Sydney Harbour occurs in Newington Nature Reserve

(~6 ha), but over 70% of the 757 patches identified are small (<1 ha) and isolated (Kelleway *et al.* 2007). Seagrasses have also declined in extent and are now estimated to occupy less than half the area (~51.7 ha) they did in 1943 (West *et al.* 2004). In contrast, mangroves have increased their distribution, being relatively uncommon until the 1870s (McLoughlin 2000). Their mapped extent has continued to increase between the 1940s and the 2000s (West *et al.* 2004), with the current estimate being nearly 184 ha. Mangroves have replaced saltmarsh in many places in the Harbour (Kelleway *et al.* 2007) and such changes in the distribution of these habitats are a global trend (Saintilan *et al.* 2014). Mangroves have increased in coverage at, or near, their poleward limits on at least five continents, usually at the expense of saltmarshes (Saintilan *et al.* 2014). This is partly as a result of changes in climatic conditions and, to some extent, to local stressors such as sedimentation, pollution and habitat modification. Seagrasses have also been declining globally (Waycott *et al.* 2009). Seagrass coverage in Chesapeake Bay, for instance, an important drowned valley estuary in USA, has considerably declined over the past 30 years and such declines have been attributed to deteriorating water quality (Orth *et al.* 2010). Understanding the extent of these changes and their full consequences to the local diversity and the functioning of systems is crucial for the development of effective conservation policies.

Open water habitats

Open water is a major habitat in estuaries and marine embayments. The contribution of this habitat to sustaining biodiversity and ecosystem function is well recognised through its role in the

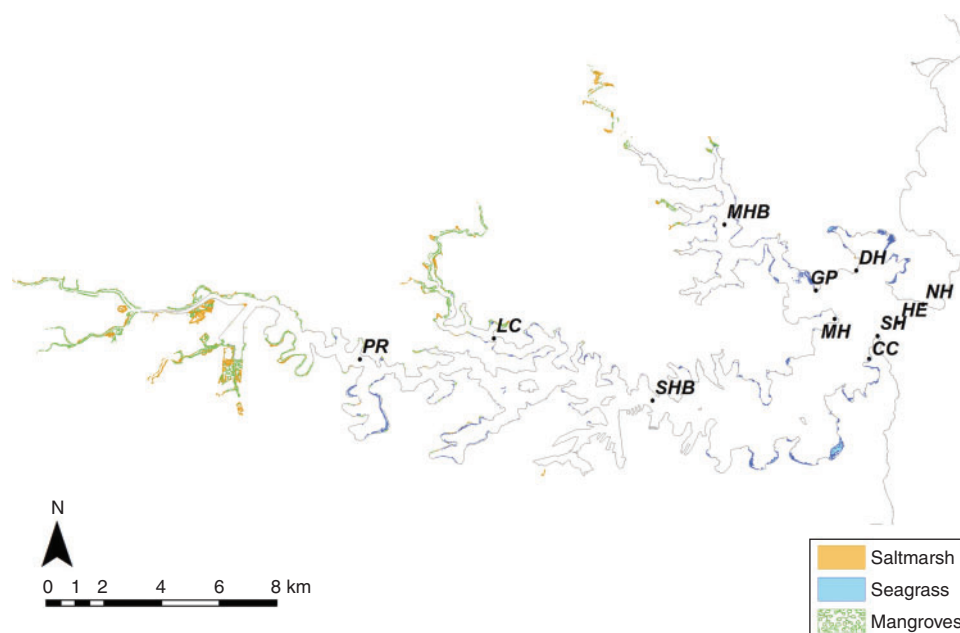


Fig. 4. Map of the distribution of the macrophytes habitats (i.e. seagrasses, mangroves and salt marshes) in Sydney Harbour and some geographical points (mentioned in the text). CC, Camp Cove; DH, Dobroyd Head; GP, Grotto Point; HE, Harbour Entrance; LC, Lane Cove; MH, Middle Harbour; NH, North Head; PR, Parramatta River; SH, South Head; SHB, Sydney Harbour Bridge.

transport, dilution and transformation of dissolved and particulate materials that impact estuarine ecology (Connolly *et al.* 2005). It also provides habitat for planktonic food webs (Cloern 2001), facilitates life stage transitions for meroplankton and fishes (Potter and Hyndes 1999) and acts as a corridor for the movement of species at higher trophic levels such as fishes and mammals (Gillanders *et al.* 2011; Gaos *et al.* 2012). The species in these habitats span orders of magnitude in terms of size (microorganisms to mammals; micrometres to tens of metres) and spend at least part of their lifecycle in the water column with little direct interaction with the benthos. For the purposes of this review, we do not consider organisms attached to free floating debris or watercraft to be open water biota (Widmer and Underwood 2004).

Although, Sydney Harbour is home to 586 species of fishes, most studies on fishes have generally focussed on benthic reef dwelling species, or on the effects of commercial and recreational fishing in the Harbour (Clynick 2008a; McKinley *et al.* 2011). Most of the latter have, however, focussed on the by-catch of trawling or did not specify which capture methods were used, so very little information on pelagic fish is available. Researchers in Sydney have been working to address this significant gap and publications on the fauna, specifically fishes, of open water habitats should be available in the next few years.

Studies of phytoplankton in Sydney Harbour have been limited to those on saxitoxin producing species involved in harmful algal blooms (Murray *et al.* 2011), which pose a threat to NSW oyster industry. Ajani *et al.* (2001) reviewed the data on blooms of toxic and harmless algae along the NSW coast and found that, although toxic algae have been reported from Sydney Harbour since European colonisation, blooms have been historically rare. This is in contrast to Chesapeake Bay, USA, and many harbours in Hong Kong, which have reported history of frequent harmful algal blooms (e.g. Glibert *et al.* 2001; Yin 2003). Some of the potentially harmful species of microalgae and dinoflagellates recorded in the Harbour include *Alexandrium catenella* and *Chattonella gibosa*, which have had three reported outbreaks from 1983 to 1999 (Ajani *et al.* 2001). *C. gibosa* is linked to high mortality of yellowtail and sea bream, as well as farmed bluefin tuna (Marshall and Hallegraeff 1999). Other unidentified blooms in Sydney Harbour have been reported since European colonisation, but our limited taxonomic knowledge has meant these blooms have gone without study, and their potential effects are unknown (Ajani *et al.* 2001). *Scrippsiella trochoidea* and *Gonyaulax polygramma* have also been recorded in Sydney Harbour and, although not toxic, can grow to such densities as to create anoxic conditions in the water column. During the period between 1890 and 1999, several outbreaks of harmless microalgae occurred, including *Gymnodinium sanguineum* (1930–32), *Trichodesmium* sp. (1984) and most recently *Noctiluca scintillans* (1999). These blooms had no discernible impact on either human health or the ecology of Sydney Harbour and simply discoloured the water (Ajani *et al.* 2001). There are no published studies on zooplankton in Sydney Harbour.

Sydney Harbour is also home to one of only five Little Penguin (*Eudyptula minor*) colonies on the south-east coast of Australia. This colony is located along the northern foreshore of the Harbour from Manly to North Head (Priddel *et al.* 2008). In 2005, there were ~56 breeding pairs in the Sydney colony

(Priddel *et al.* 2008). Reports from 1912, however, indicate that this colony was much larger (Priddel *et al.* 2008).

Studies of other open water macrofauna, including large mammals, are either completely lacking or not presently published, although there are periodic sightings of humpback and Southern Right whales in the Harbour during the months May–September. There is an ongoing acoustic tagging study of Bull Sharks, *Carcharhinus leucas*, that indicates this species makes regular visits to many parts of the Harbour (NSW Government unpubl. data), but the results are as yet unpublished.

Discussion and knowledge gaps

Although Sydney Harbour is a hotspot of biodiversity, there have been few long-term, comprehensive studies of the habitats and organisms of the Harbour. Important habitats such as beaches remain unstudied and many ecological processes have not been investigated. Here we discuss our current understanding and highlight the most pressing knowledge gaps.

Long-term trends

There have been few temporally replicated sampling studies of the ecology and biodiversity of Sydney Harbour and we identify this as a high priority knowledge gap. Long-term datasets are important to establish the dynamics of an ecosystem and understanding how systems have changed in the past is crucial for accurate and sensible predictions of future changes (Holmes 2006). Measurements collected over decades and historical records dating back centuries provide important insights and evidence about the environment today, and how it may respond to predicted changes (e.g. Holmes 2006). Past changes in water quality or the introduction of a pest species, for example, affect the structure and functioning of systems with consequences for the current biota. Long-term data series can also illustrate how ecosystems respond both to natural processes and human activities. Environmental managers are in a much better position to develop effective conservation strategies when in possession of quality long-term biological and physical data (Christensen *et al.* 1996).

One of the few temporally replicated datasets for Sydney Harbour describes the distribution of soft sediment macrophytes (McLoughlin 2000; West *et al.* 2004; Kelleway *et al.* 2007). Records have shown that saltmarshes and seagrasses have significantly declined in the last decades, while mangrove distributions have increased. Some reasons hypothesised for these changes are contamination, changes in sedimentation and climatic changes (Mayer-Pinto *et al.* 2015). These systems are intrinsically different in their structure and function, each supporting very distinct communities. The increase in distribution of mangroves does not, therefore, offset the decrease of saltmarshes and seagrass, which should be considered a high priority conservation issue. The observed shifts in the distribution of soft sediment macrophytes are likely to have important implications for the diversity and functioning of Sydney Harbour.

Biophysical interactions

To be effective, ecosystem-based management requires an understanding of the variables that determine the structure and

function of biological assemblages within a given habitat and the expected range of interactions between the biological and physical aspects of the system (e.g. [Ranasinghe *et al.* 2012](#)). In the Harbour, there is an important knowledge gap surrounding the biophysical interactions between sediment type and benthic diversity. The distribution of infauna is strongly influenced by sediment characteristics ([Hutchings 1998](#); [Snelgrove *et al.* 1999](#)), which, in turn, is often determined by physical processes. Infauna and sediment microbes play a critical role in the biogeochemical cycling of nutrients and organic matter, and form a fundamental part of food webs. In addition, they represent a substantial proportion of the macro- and micro-diversity of the Harbour, yet only four papers paid any attention to the fauna of the Harbour's 42 sandy beaches. A comprehensive survey of the structure and function of soft sedimentary habitats (including intertidal beaches) is required.

Microfauna

Despite the acknowledged role of microbes in maintaining ecosystem function, our understanding of bacterial communities in the Harbour is in its infancy. For instance, the two studies of microbes in the Harbour sediments focussed solely on structural aspects of these communities. Marine organisms live in a 'soup' of 10^6 bacteria and 10^7 viruses per millilitre ([Reinheimer 1992](#)) and eukaryotes need an associated microbial community for normal functioning ([Rosenberg *et al.* 2007](#)). Moreover, microbes play essential roles in regulating the biogeochemical processes of the ocean, e.g. through nutrient cycling, thus making it imperative to understand the mechanisms by which environmental factors affect their community structure and how that translates into changes in whole ecosystem functioning ([Azam and Malfatti 2007](#)). New technologies now allow the study of the genetic composition of whole communities of microbes, transforming our understanding of the diversity and function of microorganisms in the environment. As eukaryotes need an associated microbial community for normal functioning, there is an increased understanding that micro- and macroorganisms should be studied in conjunction as associational units of host and microbiome, or 'holobionts' ([Rosenberg *et al.* 2007](#)). Sequencing technologies have driven cost-effective analysis of gene expression in eukaryotes, providing an innovative new perspective on, not only the responses of marine organisms to their environment ([Fan *et al.* 2013](#)), but also the consequences to the environment associated with their presence or absence. Increasing our knowledge of micro-macro interactions will help us to create a holistic and therefore, improved understanding of the processes occurring in Sydney Harbour.

Pelagic environments and hydrology

Our understanding of the biodiversity and functional significance of the open waters within Sydney Harbour is limited. It is clear that water quality in Sydney Harbour (as defined by Chl-*a* concentration, turbidity, dissolved nutrients) generally increases from upstream to downstream, and is strongly dependent on rainfall because of stormwater inputs and sewer overflows ([Robinson *et al.* 2014](#)). How this influences carbon and oxygen

fluxes, and the implications for higher trophic levels have, however, been little investigated. Knowing how a range of organisms behaves (particularly in relation to feeding) and moves through open water habitats is essential to understand food web structure and maintain the biodiversity of the Harbour. In San Francisco Bay, for instance, shifts in the north-west Pacific Ocean from a warm to cold phase alter the immigration patterns of predators into the bay ([Cloern *et al.* 2007](#)). Similarly, changes in near and offshore oceanography, including increased influence of the EAC, have the potential to strongly influence the open water habitats of Sydney Harbour.

There are also knowledge gaps regarding abiotic parameters of the Harbour. To date, no published circulation modelling studies investigate the interactions between the EAC offshore, coastal waters and the circulation within the estuary. Limited data exist on water movement at the entrance to the Harbour, but little eastward of this boundary. Thus, we have no information on the fluxes of oceanic water masses and associated nutrients into the Harbour and movement of nutrients and fresh water out of the Harbour into coastal waters. This could have important implications for the heat, mass and nutrient budgets within the estuary. Furthermore, there have been limited modelling studies investigating freshwater inflow. Coupling these two forcing mechanisms in a modelling framework would provide the basis for realistic forecast scenarios and thus significantly improve our understanding of estuarine ecosystems.

Finally, the importance of sediment quality to the quality of overlying waters also needs further study if we are to accurately parameterise water quality models and understand the value of potentially remediating or capping polluted sediments.

Integrating the physical and biological aspects

In order to understand how Sydney Harbour 'works', it is necessary to understand how its biological, chemical and physical processes interact within the Harbour and how these factors are affected by the larger environmental context of Sydney Harbour. Although we can treat each natural habitat within the Harbour as a discreet system, in reality, fluxes of matter and energy are exchanged between habitats. Such connections differ in their importance and magnitude and may act over large temporal and spatial scales. The interactions among the physico-chemical and biological properties of systems have important implications for the structure and function of ecosystems. The dynamics of marine food webs, for instance, are determined not only by biological properties of habitats such as composition, distribution and biomass of species at different trophic levels, but also by the physical structures and processes regulating the system such as currents, geology, bathymetry, etc. (e.g. [Denman and Gargett 1995](#)). Such processes regulate, among other things, the supply of dissolved nutrients to the surface layer of the water column (i.e. food availability for the plankton) and the thickness of the surface mixed layer, thereby controlling the light levels on which the phytoplankton depend to photosynthesise ([Palmer *et al.* 2000](#)). Furthermore, the species composition of a certain area may be determined by such bio-geo-physico-chemical interactions (e.g. [Palmer *et al.* 2000](#)), making it crucial to have a full understanding of how these processes integrate and

feedback on each other. A deeper understanding of the spatial and temporal context of connectivity within the Harbour is therefore pivotal if we want to increase our predictive ability (Thompson *et al.* 2001) and management efficacy.

We must also consider the importance of the somewhat unique environmental context surrounding the Harbour when understanding its high biodiversity. Sydney Harbour sits in a highly oceanographically dynamic location which is variously influenced by the tropically originating EAC and the numerous cyclonic and anticyclonic eddies shed by meanderings of the EAC (Everett *et al.* 2012). Although the EAC is capable of delivering larval fish from the tropics to the Sydney region (Booth *et al.* 2007; Feary *et al.* 2014), local eddies are capable of trapping and recirculating larvae near the shelf. The nature of the eddy (cyclonic v. anticyclonic) can, however, have profound consequences for the health of the entrained larvae (Mullaney and Suthers 2013; Everett *et al.* 2015). Modelling studies by Roughan *et al.* (2011) show that over a 14-year period, larvae, eggs and spores could arrive in Sydney Harbour from both long and short distances from either the north or the south. The work highlighted the dynamic nature of the region, showing that particle retention and recirculation was maximal when eddies were present, southward transport was maximal during periods when the EAC remained attached to the coast, and northward shelf flows are stronger in winter, and in the absence of EAC eddies.

This dynamic environment sets the stage for the supply of propagules from a very broad latitudinal range and a variety of habitats. Thus although Sydney Harbour does have high diversity compared with other urbanised estuaries even for individual surveys at specific points in time, there is little doubt that the uniquely high lifetime richness of the Harbour is the result of the accumulation of species over time from this very broad region of influence. It is thus essential that we develop a deeper understanding of the spatial and temporal context of both the external and internal connectivity of the Harbour if we want to increase our predictive ability (Thompson *et al.* 2001) and management efficacy.

Conclusion

Sydney Harbour is a hotspot for marine diversity, having a relative greater number of species and habitats than most of the harbours and estuaries in Australia and worldwide. This is the first comprehensive synthesis of the biophysical and ecological aspects of the Harbour. Our current knowledge of the ecology of the habitats encompassed by Sydney Harbour, and consequently, the ecosystem services provided, is patchy, with many critical gaps that need urgently to be filled. A sound ecological understanding of the system functioning, including the mechanisms and forces driving its diversity and complexity are pivotal to ensuring the sustainable use of this estuary for the well being of all.

Supplementary material

The Supplementary material, which contains all the reviewed studies and their classification, is available from the journal online (see http://www.publish.csiro.au/?act=view_file&file_id=MF15159_AC.pdf).

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