REVIEW

An ecosystem ecology perspective on artificial reef production

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Abstract

1. Artificial reefs are used around the world for many purposes, including widespread deployment to increase fishery yields. These reefs are well-studied from a direct fisheries-based perspective, drawing largely on traditional theory and methodological approaches from population and community ecology.

2. Here we provide an alternative perspective using basic tenets of ecosystem ecology. We focus largely on primary production, as this ecosystem process necessarily constrains the secondary production of fish and invertebrates.

3. We use this ecosystem ecology viewpoint to examine the long-standing attraction/production question—do artificial reefs support 'new' fish production or simply attract individuals from other habitats? Central to this discussion is identifying ecological thresholds and self-reinforcing feedbacks. For example, biological or physical processes may facilitate reaching nutrient supply thresholds where fundamental ecological dynamics are shifted, such as enhanced seagrass allocation of resources to above-ground plant structures following aggregation of fish around reefs.

4. *Synthesis and applications.* We propose that the scope for enhanced primary productivity (or other accelerated ecosystem processes) is an under-utilized guideline that can be used to prioritize artificial reef deployment as part of broader coastal management programmes. Such an ecosystem ecology perspective may provide new insights into the ecological role of artificial reefs and guide the optimization of their deployment and management.

KEYWORDS
artificial reef production, decomposition, food webs, marine fisheries, nutrients, primary production, reefs, threshold effects

1 | INTRODUCTION

Predicting the overall productivity of an ecosystem is a long-standing challenge in ecology and conservation biology. Understanding controls of primary production is important in both theoretical and applied contexts, as it bounds the total amount of production, across all trophic levels, which a given system can support (Geider et al., 2001). Secondary production (of all consumers in an ecosystem) is, in most systems, tied directly to net primary production (NPP) and how energy/biomass is passed through subsequent

trophic levels (Lindeman, 1942). As such, one starting point for estimating the amount of secondary production supported within an ecosystem is the quantification of NPP, as well as identifying the factors that mediate it.

Biological, chemical and physical factors can limit NPP in terrestrial and aquatic systems (Geider et al., 2001). In marine ecosystems, primary constraints on NPP include nutrient supply, light penetration and substrate availability (for benthic primary producers), with the relative importance of these factors varying among ecosystems and constituent species. For example, phytoplankton

production in the world's oceans is dependent on spatial and temporal patterns in nitrogen, phosphorus and iron availability, along with species-specific stoichiometric requirements (Coale et al., 1996; Falkowski, Barber, & Smetacek, 1998; Tyrrell, 1999). In turn, oceanic fishery production is determined by how this primary production is assimilated by consumers, reliant on the efficiency of energy transfer, bioenergetics constraints and consumer stoichiometry (Chassot et al., 2010). Understanding the mediators of NPP in marine ecosystems is thus a necessary step towards understanding local and global constraints on fishery productivity (Ryther, 1969).

Employing NPP as a starting point for examining marine fishery production is less common than direct population/community perspectives. That is, fisheries research often is focused (rightfully) on quantifying fish density, biomass, growth, community composition or other metrics relating directly to the species of interest. An ecosystem ecology perspective provides a valuable complement to exploring controls on fishery production. Central to ecosystem ecology is the flow of energy/nutrients through components of an ecosystem, and we frame this paper accordingly. We focus on artificial reef systems to explore controls on fishery production using primary production as a lens. We frame the discussion around a key issue in marine fishery management—the 'attraction/production' question regarding artificial reef deployment. We discuss the importance of alleviating resource limitation at the base of the food web, as well as identifying ecological thresholds and positive feedback cycles, associated with reef deployment.

2 | ARTIFICIAL REEF PRODUCTION

The decline in marine fisheries has emerged as one of the world's foremost environmental crises (FAO, 2014). Despite few actual extinctions, fish stocks have been depleted compared to historic levels (McCauley et al., 2015). With the world's population expected to grow by another 2 billion by 2050, and per capita consumption of fish increasing concomitant with rising standards of living, demand on fisheries resources will only intensify. In this context, it is evident we need to assess how coastal zone management practices could help stem fishery declines and/or lead to their recovery. Artificial reef deployment is one approach that may be relevant to this end.

Artificial reefs are broadly defined as any submerged structures placed on substratum to mimic some characteristics of a natural reef, altering physical, biological and/or socio-economic variables related to marine resources (Seaman, 2000). Some structures are designed for other purposes, yet effectively function as artificial reefs, for example, jetties or piers (we adopt this broad consideration of 'artificial reef' herein). It is well known that artificial reefs typically result in dense aggregations of fish. This has been documented across systems and a range of spatial scales, from small concrete block reefs in shallow coastal areas (Yeager, Allgeier, & Layman, 2011) to massive deep-sea oil rigs (e.g.

Macreadie, Fowler, & Booth, 2011; van Elden, Meeuwig, Hobbs, & Hemmi, 2019; see example artificial structures in Figure 1). It has been suggested that oil and gas platforms off the coast of California have the highest fish production per unit area of any marine habitat world-wide—as much as an order of magnitude greater than other high productivity marine ecosystems (Claisse et al., 2014).

The dense fish aggregations may be driven by many factors, including simple attraction of fish from surrounding areas or shifting environmental dynamics such that they support additional fish production. Often these two mechanisms are couched in a context of 'attraction' versus 'production' (Bohnsack, 1989; Powers, Grabowski, Peterson, & Lindberg, 2003). That is, are fish primarily moving to the new structure from other areas (i.e. the attraction hypothesis)? Or does deployment of artificial reefs lead to changes in recruitment rates, food web structure or ecosystem processes, allowing fish secondary production to be augmented to levels otherwise not attainable (i.e. the production hypothesis)? If artificial structures do provide for additional fish production, reef deployment could become a core component of attempts to increase fishery yields. But if they primarily serve as fish attractors, artificial reefs may facilitate over-exploitation by making extraction easier for fishers. A dichotomous view of attraction versus production is over-simplified, as there is a broad continuum balancing these two alternative mechanisms. Finding where artificial reefs fall along this continuum remains a critical question for fishery managers, yet continues to be a rather difficult question to address in practice.

Evaluation of artificial reef deployments typically revolves around the direct study of the fish or invertebrates that are supported by that reef. One of the traditional tenets in the artificial reef literature is that there are five general ways by which artificial structures may result in increased fish biomass (quoted from Bohnsack, 1989): '(a) providing additional food, (b) increasing feeding efficiency, (c) providing shelter from predation, (d) providing recruitment habitat for settling individuals that would otherwise have been lost to the population and (e) indirectly, because fish moving to artificial reefs create vacated space in the natural environment that allows replacement from outside the system'. All these mechanisms are critical in assessing artificial reef function and they relate to shifts in population/community processes.

Core to the question of whether artificial structures result in 'new' fish biomass is quantifying secondary production—accumulation of animal biomass over time. Powers et al. (2003) outline a comprehensive approach to assess the relative importance of attraction and/or production for fish on artificial reefs, employing data on fish density, length-frequency distributions, diets, behaviours, age-specific growth, mortality rates and residency patterns. Likewise, Claisse et al. (2014) used fishery-independent data, size structure, changes in biomass and recruitment data to assess secondary production on oil and gas platforms. In both studies, and most others quantifying secondary production, population- or community-level measures are necessarily used. Yet even in cases when these data are available and robust, discerning

FIGURE 1 Structures that fall within a broad classification of artificial reefs: (a) a reef ball immediately after deployment on New Providence Island, The Bahamas; (b) one of the pieces in the Sir Nicholas Nuttall Coral Reef Sculpture Garden, New Providence Island, The Bahamas; (c) Katrina Reef off the coast of Mississippi, made of limestone and crushed concrete—see Mazzei and Biber (2015); (d) one component of an artificial reef complex deployed in Daya Bay, China—see Yu et al. (2015); (e) the Tibbetts, a Russian frigate that was sunk in the waters of Cayman Brac, Cayman Islands and (f) oil and gas platform in the South China Sea. Photograph credits are listed in Acknowledgements
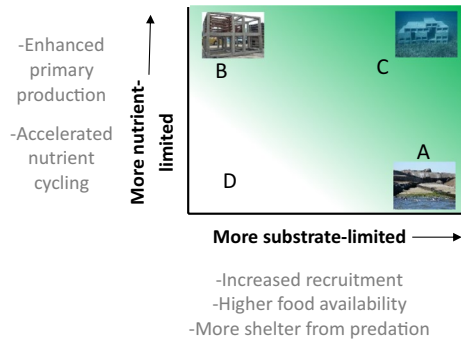

between attraction and production scenarios remains challenging, largely because it must be definitively shown that fish populations are not declining in areas adjacent to the artificial structures. This is difficult because of the heterogeneous nature of marine ecosystems, ecosystem connectivity, variable temporal dynamics, identifying relevant spatial scales of study and lack of suitable controls.

Here we take an ecosystem-based perspective to examine the attraction/production question using a different lens. We avoid discussion of changes in fish population dynamics, community structure and trophic ecology, as these are common areas of study in the field and have been reviewed many times. Instead, we identify how primary production and other ecosystem processes can be altered by reef deployment. First, we provide examples of how reef deployment may alleviate resource limitation, focusing on substrate availability and nutrient cycling. We then discuss two concepts, threshold responses and positive feedback cycles, that can be used to frame an examination of ecosystem-level processes (e.g. primary production, nutrient cycling) driving enhanced production.

3 | AXES OF RESOURCE LIMITATION

3.1 | Constraints on primary production

Identifying constraints on primary production is a central objective in the field of ecosystem ecology. And given that secondary production is usually tied closely to NPP (Lindeman, 1942), it is a logical inference that enhanced NPP would be linked to higher levels of secondary production within ecosystems, including on and around artificial reefs. Following reef construction, new autotrophic resource pathways can be incorporated into food webs primarily by (a) providing additional substrate for plants or algae (as well as a new substrate for filter-feeders consuming pelagic autotrophs); (b) enhancing ambient nutrient availability; or (c) both mechanisms acting together (Figure 2). Yet few studies have quantified characteristics of autotrophic communities directly on artificial reefs. Studies that examine autotrophs focus largely on autotroph community composition (e.g. Andersson & Ohman, 2010; Choi, Takeuchi, Terawaki, Serisawa, & Ohno, 2002; Leitão, 2013; Wilhelmsson & Malm, 2008),

-Enhanced
primary
production

-Accelerated
nutrient
cycling

More nutrient-limited ↑

More substrate-limited ⟶

-Increased recruitment
-Higher food availability
-More shelter from predation

FIGURE 2 Two axes—substrate and nutrients—delineating constraints on primary productivity in an ecosystem. The background colour represents the scope for primary productivity enhancement associated with artificial reef deployment; darker green represents sites with a higher scope for increases in productivity with reef deployment. Letters represent scenarios where primary production is primarily substrate-limited (A), nutrient-limited (B) or limited by both resources (C). Pictures are provided of existing artificial reefs that represent these scenarios—the text has a description of each of these examples. Point D represents a habitat that is replete with nutrients and has abundant structural complexity, a scenario where artificial reefs are least likely to lead to substantial increases in productivity (and thus no example reef image is included). Potential mechanistic drivers related to each resource axis are in grey text

with much less attention paid to consequences of shifts in primary production or other ecosystem processes. We acknowledge that such axes of resource limitation are continuous, yet we introduce specific examples from a categorical perspective to demonstrate how artificial reef deployment may alleviate resource limitation in general contexts (Figure 2).

3.2 | Substrate availability

Marine ecosystem productivity may be constrained in circumstances where, although nutrient availability is high (fuelling high levels of pelagic primary productivity), substrate is lacking to provide settlement sites for benthic organisms. In such situations, artificial reefs could enhance secondary production, as mediated through primary production, in two ways. First, they provide additional attachment locations for macroalgae and substrate area for microalgae and other autotrophic constituents of associated biofilm (Salamone, Robicheau, & Walker, 2016). Second, they enhance settlement of sessile filter-feeders, organisms utilizing pelagic autotrophic production. The contribution of sessile filter-feeders can be locally significant, creating different pathways to bring primary production into reef-associated food webs. In the Mississippi Sound (USA), Mazzei and Biber (2015) discuss such food web shifts (inset reef in Figure 2A). Benthic secondary production was enhanced via accelerated benthic gross primary production, as well as through increased benthic-pelagic coupling by filter-feeders (translocating nutrients

and energy to the benthos). This new benthic production is then directly available for higher order consumers (Mazzei & Biber, 2015).

In the nutrient-rich waters off the coast of California, hard bottom habitat is often absent, limiting the distribution of kelp *Macrocystis pyrifera* due to lack of attachment sites. Restoration initiatives create artificial structures to increase suitable substrate for kelp attachment (Deysher, Dean, Grove, & Jahn, 2002). In some cases, this can lead to substantial increases in fish diversity and abundance (Reed, Schroeter, Huang, Anderson, & Ambrose, 2005; Schroeter, Reed, & Raimondi, 2015). Both the Mississippi Sound and California kelp examples illustrate the emphasis on changes in community structure for assessing food web alterations following reef construction. We suggest a critical gap remains: quantifying changes in ecosystem processes that may be used to link artificial substrate deployment to the end goal of assessing if and how secondary production can be augmented.

3.3 | Nutrient availability

Enhanced primary production via increased nutrient supply rates can be driven by artificial reef-driven shifts in local hydrology (Lung-Liu & Su, 2013). One example of this is the use of larger structures in deeper waters that disrupt horizontal currents and force water vertically. Since nutrient levels are typically higher in the aphotic zone in deeper waters (as well as in the benthic environment in coastal waters), vertical water movement serves to recirculate nutrients back to the upper levels of the water column. This can be especially important during the summer in temperate regions when stratification limits vertical mixing and nutrients are trapped at depth (Kim & Shimasaki, 2013). For example, in the Uwa Strait, Japan, concrete walls (95 m in length and 10 m high) were specifically designed to induce upwelling and have served to increase chlorophyll *a* concentrations above these walls two to three fold (Suzuki & Hashimoto, 2011). Following the construction of an artificial reef in the Bongo River of Japan (42 m × 17 m × 129 m), the standing crop of phytoplankton and zooplankton increased 50-fold and 2.3-fold respectively (Jeonga, Leeb, Park, Kimc, & Kimb, 2013). In Daya Bay, China, reef complexes were constructed using a series of 3 m × 3 m × 3 m structures (one is shown in Figure 1d and the inset in Figure 2B; total reef dimensions 966 × 2,850 m²), resulting in a total of 91,500 m² of new surface area (Yu, Chen, Tang, & Qin, 2015). Effects on water column productivity could be detected from space, including chlorophyll *a* concentrations elevated up to 4.9 km away from the reef complex (Yu et al., 2015). Such findings suggest the large spatial scales at which artificial reef deployment could be relevant. Coupled with smaller scale studies that are necessary to elucidate specific ecological mechanisms (such as those in the case studies detailed in the following sections), possibilities of new ecosystem-scale secondary production associated with reef construction become evident.

The example of altered hydrology affecting nutrient cycling also brings to light an aspect of artificial reef ecology that should be acknowledged, namely, that reefs are 'open' systems and not patches isolated from organism and material movements. Though we will not discuss this topic extensively, a key point in the context of this review is that reef deployment may alter bottom-up processes in a way that alters local productivity or other ecosystem processes. It is not necessary to demarcate the relative contribution of local versus external drivers to recognize shifts in ecosystem processes that occur because of reef deployment. To fully encapsulate artificial reefs' role across entire coastal seascapes, an even more inclusive view of habitat and ecosystem linkages is warranted.

3.4 | Dual resource limitation

In many shallow water systems of the tropics, there may be both a lack of structure and relatively low ambient nutrient levels. Artificial reefs may serve to alleviate both of these limiting resources, resulting in an interactive effect that leads to significant shifts in ecosystem processes (Allgeier, Yeager, & Layman, 2013; Layman, Allgeier, Yeager, & Stoner, 2013). For example, in shallow (<4 m), oligotrophic, seagrass ecosystems of The Bahamas that are often devoid of structure, fish densities are relatively low and individuals are spread across the seascape (Allgeier, Layman, Mumby, & Rosemond, 2014). Following the construction of cinder block reefs (inset in Figure 2C), fish aggregate around the structures (Figure 3). Many of the fish remain close to the reef during the day and forage in adjacent seagrass or sand habitats at night (Meyer, Schultz, & Helfman, 1983; Yeager et al., 2011). During daytime hours, this results in concentrated nutrient supply (particularly nitrogen and phosphorus) through fish excretion and egestion. As such, fish can serve as primary vectors of nutrients, translocating them from adjacent seagrass-dominated benthos (distances of ~10–100s of metres) to the immediate vicinity of the reef, thereby enhancing localized primary productivity. For example, Allgeier et al. (2013) found a 300+% increase in seagrass growth rate adjacent to reefs with aggregating fish relative to areas with no structure.

There may be a similar role of planktivorous fish in recycling nutrients to benthic habitat (Morais & Bellwood, 2019). For example, planktivorous damselfish feed on zooplankton supplied by prevailing currents and then supply nutrients to the benthic environment through excretion and egestion, nutrients which have been shown to facilitate growth in coral (Holbrook, Brooks, Schmitt, & Stewart, 2008) and kelp (Bray, Purcell, & Miller, 1986). Since planktivorous fish can reach extremely high densities on artificial structures, especially those with significant vertical structure (Arena, Jordan, & Spieler, 2007; Charbonnel, Serre, Ruitton, Harmelin, & Jensen, 2002; Paxton, Taylor, Peterson, Fegley, & Rosman, 2019; Rilov & Benayahu, 2002), the importance of their nutrient translocation role warrants further study.
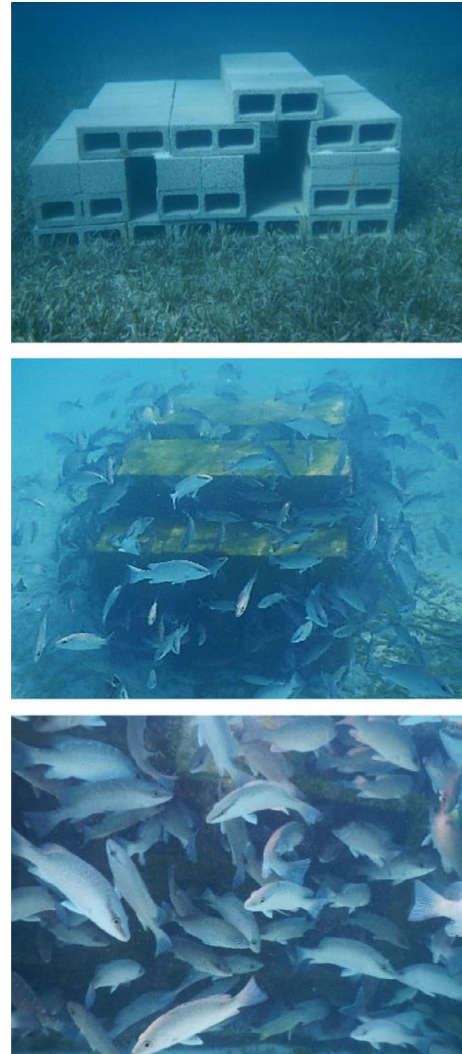
FIGURE 3 An artificial reef made from 84 cinder blocks on the west coast of Andros Island, The Bahamas. This area is one of the least fished in the Wider Caribbean region and is characterized by oligotrophic waters and virtually no structural features. One year after deployment, this small reef supported hundreds of adult fish, dominated by gray snapper *Lutjanus griseus*

4 | ECOLOGICAL THRESHOLDS AND POSITIVE FEEDBACKS

4.1 | Ecological background

For artificial reefs to augment fish production, fundamental shifts in population dynamics, species interactions and/or ecosystem processes must occur. As alluded to above, the traditional approach to assess shifts in secondary production is to quantify the role of the structures in affecting population dynamics or species interactions. But shifts in ecosystem processes may be just as important. Two ecological concepts are especially relevant when considering this ecosystem ecology perspective. First, ecological thresholds—specific tipping points at which an environmental driver(s) causes dramatic shifts in community or ecosystem states

(Kelly et al., 2015; Suding & Hobbs, 2009); small changes in an environmental driver leads to large changes in ecosystem processes in a nonlinear fashion (Groffman et al., 2006). Second, in many cases, these dramatic shifts are driven by feedbacks, that is, effects of a perturbation continue to intensify through self-reinforcing mechanisms, driving a system away from an initial starting point. We discuss two examples of how such mechanisms may relate to enhanced production following artificial reef construction (Figure 4).
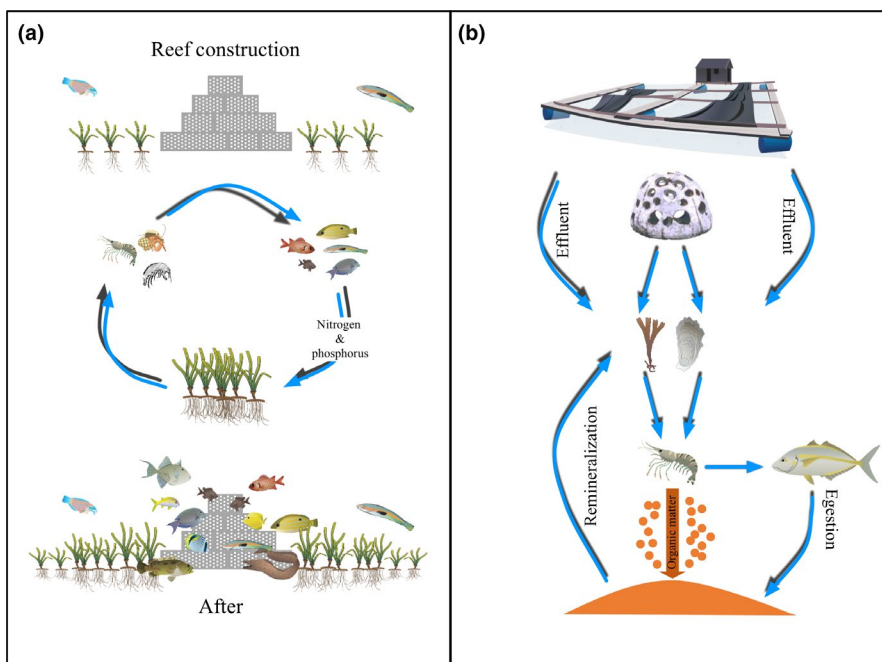
4.2 | Seagrass ecosystems

Artificial reefs in shallow seagrass beds of The Bahamas lead to a concentrated supply of nutrients from aggregating fish (see the previous section). This sets in motion a set of self-reinforcing feedbacks linking primary and secondary production (Figure 4a). Nutrient translocation drives increased seagrass and algal productivity, as well as changes in seagrass traits (e.g. increased shoot density and longer blades). The seagrass bed then can support greater production of invertebrates and small fish, due to greater availability of food resources and the increased structural complexity of the seagrass canopy (which, in turn, provides additional substrate for algal growth). This is reflective of fundamental links between primary and secondary production (Lindeman, 1942). Increased secondary production of small consumers provides a larger forage base for other predators (Yeager, Acevedo, & Layman, 2012). Nutrient cycling continues to accelerate as faunal densities increase, driving positive feedbacks and creating a distinct biogeochemical hotspot in the seascape (Layman et al., 2013).

Critically, the relationship between above-ground seagrass production and nutrient supply is highly nonlinear, leading to key ecological thresholds. High densities of aggregating fish on artificial reefs can increase nutrient supply (from fish excretion/egestion) to a critical level where seagrasses allocate proportionally more nutrients to above-ground productivity. With the same number of fish dispersed at low densities over seagrass beds (see Allgeier et al., 2014), nutrients from fish are not concentrated sufficiently and seagrasses primarily shunt nutrients to below-ground structures, consistent with strategies of terrestrial plants in low nutrient soils. Due to reef deployment, above-ground seagrass biomass/production (as well as for associated algal communities) can be higher than if nutrients were widely dispersed (even when summed across the entire seascape). The above-ground increases in productivity and structural complexity are what give rise to the positive feedback cycle outlined above.

Seascape-scale patterns reinforce the idea that fundamental shifts in ecosystem processes occur following reef deployment. For example, fish abundance across artificial reefs in The Bahamas study system can be predicted by seagrass cover (at 1–100 m scales), suggesting the tight link between primary and secondary production (Yeager et al., 2011). Importantly, fish condition (white grunt, *Haemulon plumierii*, as proxied by lipid content) is positively density-dependent on artificial reefs in these seagrass beds. That is, counterintuitively, grunts have a higher condition on artificial reefs with higher fish densities. This suggests that the bottom-up effect of nutrient supply, and the shifts in ecosystem processes described above, can outweigh population- and community-level competition for resources (Yeager, Stoner, Zapata, & Layman, 2014). The ecosystem perspective provides insight into reef function, and mechanisms driving increased secondary production, which would not be apparent with traditional population or community-level approaches in fishery ecology.

(a) Reef construction — Nitrogen & phosphorus — After

(b) Effluent — Effluent — Remineralization — Organic matter — Egestion

FIGURE 4 Conceptual models of biological feedbacks associated with artificial structures in marine environments: (a) artificial reefs in shallow seagrass ecosystems and (b) artificial reefs placed adjacent to aquaculture facilities. See text for descriptions of these dynamics

4.3 | Marine aquaculture

Similar feedback dynamics may be associated with artificial reefs in other systems, including those used in conjunction with aquaculture facilities (Angel et al., 2002; Gao, Shin, Xu, & Cheung, 2008; Laihonen & Hänninen, 1997). Marine aquaculture can be associated with substantial nutrients, from excess fish feed and excretion/egestion from cultured species, leaking to the marine environment. Islam (2005) estimated that as much 462 kg nitrogen and 80 kg phosphorus are released to the environment for each ton of fish produced in aquaculture facilities (based on a hypothetical model, parameterized with published empirical data from various aquaculture facilities). This often leads to eutrophication and increased turbidity in the vicinity of aquaculture facilities, with location-specific effects highly variable (Sará, 2007). In this context, artificial reefs have been deployed under or adjacent to existing aquaculture facilities to minimize unwanted environmental impacts (e.g. impaired water quality, algae blooms) of eutrophication.

Artificial reefs used for these purposes may initiate a series of positive feedbacks leading to increased secondary production. For example, 16 concrete reefs (3 m × 3 m × 4 m; total area covered 250 m^2) were deployed around a fish culture facility near Hong Kong that covers ~4.6 ha and supports ~500 t of fish biomass (Shin, Gao & Cheung, 2011). After 1 year, the reefs supported a fouling community (e.g. barnacles, bivalves, tunicates, polychaetes, bryozoans and coral) that was estimated to sequester 2,352 kg carbon, 624 kg nitrogen and 103 kg phosphorus per year. In the Gulf of Aqaba, two artificial reef units (280 cm × 240 cm × 240 cm) were placed under an aquaculture facility (20 m depth) that supports the annual production of 1,200 t of gilthead seabream *Sparus aurata*. After 10 months, chlorophyll *a* was reduced 15%–35% relative to concentrations at control sites, with organisms on the reef (dominated by tunicates and bryozoans) estimated to sequester 240 g carbon/day (Angel et al., 2002).

The sessile invertebrate and algal matrix on reefs also provide habitat for motile invertebrates and small fish, resulting in significantly greater organism biomass per unit area relative to structure-free areas. Enhanced overall biological activity can drive a series of self-reinforcing feedbacks that shifts nutrient cycling and food web structure (Figure 4b). Organic matter around reefs accumulates through various processes, including dead organisms sinking, as well as filter-feeders removing particulate matter from the water column and re-depositing it to the benthos as faeces or pseudofaeces. This can serve to accelerate overall benthic nutrient dynamics. For example, Falcão, Santos, Drago, Serpa, and Monteiro (2009), in studies focused on ecosystem processes associated with an artificial reef system in Portugal (not associated with mariculture, but pertinent), found increased porewater nutrient concentrations and microphytobenthos production adjacent to the reefs. Enhanced benthic mineralization and nutrient regeneration were fuelled by higher organic matter content. Up to two to three times higher nitrogen, phosphorus and silica were exported from sediments, a feedback providing additional resources to the organisms on the reef

(Falcão et al., 2009; Falcão, Santos, Vicente, & Monteiro, 2007). Biomass and nutrients are then passed on to transient or resident fish (Pitta et al., 2009), whose excretion and egestion can serve to further supply nutrients to resident organisms and enrich benthic organic matter content.

The overall result is a tightly linked, productive, local floral and faunal community that can support higher levels of secondary production of resident and transient fish, due to both attraction and new production mechanisms. Fish initially are attracted to the aquaculture complex due to the export of fish feed and enhanced primary production (and enhanced food resources linked to the higher local primary production). When artificial reefs are deployed, fundamental shifts in ecosystem processes occur that allow for synergistically higher levels of secondary production. This example illustrates the interactive nature of the attraction to production continuum, showing how the initial attraction of organisms may ultimately lead to nonlinear enhancement of new production that would otherwise not be attainable.

5 | FUTURE DIRECTIONS

Examining published articles suggests the broad academic and management interest in the use of artificial reefs (see online Supporting Information). A search using Web of Science reveals that at least 130 journals (2015–2018) published articles relating to empirical artificial reef research. Topics range from how reefs should be engineered, to the quantification of particular biological variables (such as those alluded to in this paper), to socio-economic factors associated with reef deployment and management. In all of these contexts, we encourage broader collaboration between stakeholders and ecosystem ecologists, partnerships that may yield important advances concerning the role of artificial reefs in the context of fishery management. This is particularly important because different fishery management goals necessitate different reef designs (Lemoine, Paxton, Anisfeld, Rosemond, & Peterson, 2019)—designs that should consider the ecosystem processes they influence.

The examples and conceptual ideas in this paper do not provide an exact template for the trajectory of future ecosystem ecology research on artificial reefs. Instead, they suggest that numerous directions are possible that move beyond research focused on direct organism-based metrics (often fish)—a broader focus on bottom-up approaches that employ ecosystem ecology perspectives is warranted. Quantitative assessments of process, not just pattern, should be incorporated into the management and design of artificial reefs. That is, understanding how primary production and nutrient cycling change following reef construction will be critical in fully understanding how artificial reef deployment affects coastal ecosystems. Explicit links between primary and secondary production are critical, as well as how increased benthic secondary production can be incorporated into a broader view of reef function (Rouse, Porter, & Wilding, 2020). Such perspectives should also be used to inform artificial reef design from an engineering perspective, where

outcomes of novel artificial reef designs are typically assessed by traditional metrics such as species diversity and community composition (Chowdhury, Hossain, Ysebaert, & Smaal, 2020; Jayanthi et al., 2020; Liversage, 2020). Further, recent advances in marine microbial ecology provide new insights into how reef structure leads to fundamental changes at the base of the food web (Li, Wang, Yu, Bai, & Qin, 2019; Qin et al., 2019) that, in turn, may be critical for fisheries (Higgs, Newton, & Attrill, 2016).

Decisions regarding deployment of new artificial reefs (and monitoring of existing ones) necessarily hinge on the limited financial, logistical and time resources available for coastal conservation and management initiatives. What criteria should be used to justify the use of limited resources for artificial reefs as a part of broader coastal management programs? We propose that the scope for enhanced primary productivity (or other accelerated ecosystem processes) is an under-utilized benchmark that can be used to this end. At a broad level, managers should identify whether a focal system is likely to be structure- or nutrient-limited (or both) based on targeted site assessments and existing ecosystem-level data. When new data can be collected, indicators of ecosystem processes (e.g. ambient nutrient concentrations or nutrient content of primary producers) can be used to inform reef deployment. This can guide artificial reef site deployment selection even at relatively small spatial scales in a coastal area. For example, the scope for primary production enhancement and shifts in fish communities following reef deployment varies substantially among bays separated by <10 km off of Îsle à Vache, Haiti (J. E. Allgeier, unpubl. data). This is because of the existing degree of nutrient limitation in a given bay, as influenced by anthropogenic nutrient and sediment loading from that watershed. In this case, reef deployment is best targeted for those bays with lower levels of existing anthropogenic nutrient/sediment loading. Such patterns must be demonstrated through tracking ecosystem process measures (e.g. primary productivity) following reef deployment—monitoring that is critical to inform ongoing reef management.

We suggest the potential of using an ecosystem ecology perspective to explore the ecological function of artificial reefs, as well as a means (in direct conjunction with population and community approaches) to address the fisheries' attraction-production question. As an organizing principle, if primary production is enhanced relative to structure-free areas, it is a logical inference that additional secondary production can be supported as well. Empirical data on shifts in ecosystem processes associated with artificial reefs are needed, especially as artificial reefs become increasingly prevalent components of coastal resource management strategies.

AUTHORS' CONTRIBUTIONS

C.A.L. and J.E.A. conceived the idea for the paper, developed the core concept, and organized the study approach; C.A.L. compiled the relevant literature and led the writing of the manuscript; J.E.A. contributed critically to multiple drafts. Both authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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