

# A designed artificial reef is among the most productive marine fish habitats: new metrics to address ‘production versus attraction’

James A. Smith<sup>1,2</sup> · Michael B. Lowry<sup>3</sup> · Curtis Champion<sup>1,2</sup> · Iain M. Suthers<sup>1,2</sup>

Received: 20 January 2016 / Accepted: 9 August 2016  
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**Abstract** It was recently demonstrated that oil platforms are among the most productive marine fish habitats (Claisse et al. in Proc Natl Acad Sci USA 111:15462–15467, 2014). Designed artificial reef systems are similar, albeit smaller, modified habitats designed to accommodate fish assemblages. We compared fish production at a large designed reef to reported production at oil platforms. Given the focus in artificial reef research on distinguishing between new and aggregated fish production, we used a different approach to that of Claisse et al. (Proc Natl Acad Sci USA 111:15462–15467, 2014) to calculate production, based on a steady-state assumption. This assumption simplifies the analysis and distinguishes ‘local production’, ‘new production’, and ‘biomass flux’. Comparing biomass flux with standing stock biomass enables a new approach to address the production versus attraction debate, by revealing how much biomass is exposed to fishing compared to how much

has local production. The local fish production at this artificial reef was  $384 \text{ g m}^{-2} \text{ year}^{-1}$ , which is within the  $105\text{--}887 \text{ g m}^{-2} \text{ year}^{-1}$  range reported by Claisse et al., although our study included visitor species not included by Claisse et al. We estimate that the fish production new to the ecosystem may only be 4–5 % of the local production, due to the large abundance of visitor species on this reef. The annual flux of biomass across this reef was very large, ~380 times greater than the standing stock biomass, meaning that this reef is vulnerable to overexploitation from fishing. Our results show that like oil platforms, designed artificial reefs can be very productive marine habitats, but may not greatly increase the net fish production in a system. The method detailed here will allow similar studies to be done relatively simply at other marine habitats, including fish aggregation devices.

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Responsible Editor: M. Peck.

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Reviewed by undisclosed experts.

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**Electronic supplementary material** The online version of this article (doi:10.1007/s00227-016-2967-y) contains supplementary material, which is available to authorized users.

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✉ James A. Smith  
james.smith@unsw.edu.au

<sup>1</sup> Evolution and Ecology Research Centre, and School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

<sup>2</sup> Sydney Institute of Marine Science, Chowder Bay Road, Mosman, NSW 2088, Australia

<sup>3</sup> NSW Department of Primary Industries, Port Stephens Fisheries Institute, Taylors Beach Rd, Taylors Beach, NSW 2316, Australia

## Introduction

Understanding the factors contributing to the productivity of marine habitats is crucial to assess their habitat value. This understanding is especially important for human-made structures such as oil platforms and artificial reefs, as their value as productive habitats can be fundamental to any cost–benefit analysis influencing their management and perception (Bohnsack and Sutherland 1985; Shipp and Bortone 2009; Fowler et al. 2014; Claisse et al. 2015; Fowler et al. 2015). Artificial reefs are often deployed with a goal to enhance fish production (Baine 2001; Miller 2002), so quantifying this production is crucial for developing successful and responsible management programmes, and an understanding of artificial reef systems can contribute to the broader management of marine ecosystems.

Fish production is infrequently estimated for marine habitats, although recent research has shown that oil platforms, per unit area of seafloor, are likely to be among the most productive marine habitats—exceeding all surveyed natural habitats (Claisse et al. 2014). This high level of production is intuitive given their size and vertical extent, and identifies them as valuable fish habitats (Claisse et al. 2015). Artificial reefs, especially purpose-built or ‘designed’ reefs, are similar to oil platforms in being typically more complex than the surrounding environment and quickly develop associated fish biomass (Folpp et al. 2011). However, the long-running discussion of fish production on artificial reefs has been focused on whether they create new fish production or simply redistribute (‘attract’) existing production (Bohnsack and Sutherland 1985; Lindberg 1997). The difficulty in distinguishing between production and attraction, and few quantitative models describing these processes, has meant that few studies have estimated fish production on artificial reefs.

Distinguishing new production and redistributed production is notoriously difficult (Smith et al. 2015) and requires knowledge of surrounding habitats and fish movements at a range of spatial and temporal scales. Quantifying the production of the fish biomass associated with an area of habitat (e.g. Claisse et al. 2014) allows us to infer a habitat’s value to the existing fish biomass, but it stops short of addressing the dynamic nature of modified habitats by distinguishing new and redistributed fish production. Distinguishing these types of production can be done by estimating the duration of an association between fish and the modified habitat, which indicates the value of the habitat to the individual rather than simply the average standing population.

A goal of this study was to present a simple approach for estimating the fish production at a reef habitat, for comparison with the production estimates of Claisse et al. (2014), and one that can be expanded to distinguish new and redistributed fish production. Our approach is similar in principle to Claisse et al. (2014) but is based on a steady-state system which simplifies the calculations. By incorporating the time-dependent association of individual fish, our approach estimates new fish production, plus the total flux of fish biomass across a habitat, to better quantify the numerical basis of the ‘production versus attraction’ debate.

## Methods

### Types of fish production

Driven by the need for artificial reef research to address the ‘production versus attraction’ debate, we focused on creating definitions of production that could address the issue

that fish using artificial reefs can be redistributed or new to the system. It became clear, however, that redistributed fish can still be locally produced, by using the new habitat as they would any pre-existing habitat. Thus, we recommend that the redistribution or ‘attraction’ of fish be redefined in a context of fish production, and we present an approach to do so based on the duration of the association between ‘attracted’ fish biomass and the reef habitat. We define in Table 1 the types of production modelled in this article, highlighting that the comparison of local production and total biomass flux across a habitat is a new and intuitive approach to understanding ‘production versus attraction’.

### Estimating fish production

Fish production can be calculated by measuring the growth in fish over a given time period (Peterson et al. 2003), with survivorship and recruitment sometimes explicitly modelled (Claisse et al. 2014). It can also be done by assuming a steady-state population structure, which does not require size-dependent growth nor information on recruitment. A steady-state assumption is the basis of much ecosystem modelling (Christensen and Pauly 1992) and allows us to assume that relative production (i.e. the production/biomass ratio,  $P/B$ ) is equal to the instantaneous total mortality of an organism (Dickie 1972; Mertz and Myers 1998; Randall and Minns 2000). Thus, fish production at a given habitat can be measured as:

$$P_i = B_i \times Z_i \quad (1)$$

where  $P_i$  ( $\text{kg year}^{-1}$ ) is production,  $B_i$  ( $\text{kg}$ ) is fish biomass at the given habitat, and  $Z_i$  ( $\text{year}^{-1}$ ) is the instantaneous total mortality rate, for fish species  $i$ .  $Z$  can be further decomposed into the sum of natural ( $M$ ) and fishing ( $F$ ) mortality rates ( $Z_i = M_i + F_i$ ). Production for the entire fish assemblage ( $P$ ; Table 1) is simply the sum of the assemblage’s  $P_i$  values. If a marine habitat has an average fish biomass that has been estimated thoroughly across the time period for which  $P_i$  is to be applied, and the mortality (i.e. turnover) rate for species  $i$  can be estimated, then it is straightforward to estimate  $P$  for a specific area of habitat using this method.

This method was compared with that of Claisse et al. (2014) to investigate the effect of the steady-state assumption and to ensure our production results were comparable. Claisse et al. (2014) measured fish production as the von Bertalanffy-based somatic growth of an observed assemblage, after accounting for mortality in that assemblage, and summed this with recruitment production (the same process for fishes <1 year old). We were able to repeat this quite closely for our study reef, with some differences due to the limits of our data: (1) we calculated production for each fish species using an average body size rather than

**Table 1** Definitions of the various production metrics used in this article

Production/biomass metric	Definition
Local fish production ( $P$ )	The fish biomass produced at a given habitat. For an artificial reef, this includes the production that has been redistributed to the artificial reef and the new production ( $P_{\text{new}}$ ) that would not exist without this new habitat
New fish production ( $P_{\text{new}}$ )	The fish production that would not exist without this new habitat. For an artificial reef, this may occur when existing fish gain benefits (growth, survival) from the reef, and their original habitats are recolonized, resulting in a net increase in fish production due to the reef. New recruitment to the reef is also possible
Redistributed fish production ( $P - P_{\text{new}}$ )	This is the fish production that has been redistributed due to the habitat change and would still exist were the reef removed—the production would simply shift elsewhere. For artificial reefs, this production may occur when existing fish move to a new reef and benefit from this habitat as they would any natural or pre-existing reef habitat, but their old habitats are less used and the system gains no new fish production
Biomass flux ( $B_{\text{flux}}$ )	The biomass of fish that use a habitat per unit of time. Biomass flux can be used to understand the relative importance of the habitat to resident and visitor species. The higher the total flux relative to the total biomass $B$ that has local production (i.e. a smaller $B/B_{\text{flux}}$ ratio), the more vulnerable the habitat is to overexploitation by fishing
Attracted fish biomass	As typically described in the literature, the fish biomass that is redistributed ('attracted') after reef deployment and appears to associate with the reef, but none of their production is assigned to the reef (e.g. Powers et al. 2003). We feel this is probably rare, and the benefit derived for a species is proportional to the time spent at a reef. 'Attraction' is a process of biomass redistribution and one that can lead to local production. 'Attraction' should be evaluated using $B/B_{\text{flux}}$ , where a small ratio indicates a reef is attractive to a species, but the reef contributes little to their production due to the short duration of the association of individual fish with the reef

The variables are those defined in [methods](#) section

the sum of size-class-specific production estimates and (2) our estimate of recruitment production was not measured but was a fixed proportion based on the findings of Claisse et al. (2014). Further information is given in Online Resource 1.

Our comparison showed good agreement between the approach of Claisse et al. (2014) and our steady-state approach. Total fish production using the Claisse et al. method was 91 % of our approach, and we feel confident the two approaches can be compared. We also feel that the Claisse et al. method will be generally more conservative than ours because the somatic growth of fish that do not survive the entire modelled period (1 year) is not accounted for in their approach but is in ours.

### Estimating new fish production and biomass flux

Identifying new and redistributed biomass or production has long been a focus of artificial reef research (Bohn-sack 1989; Bortone 2006; Smith et al. 2015), and we can approximate the production that is new ( $P_{\text{new}}$ ; Table 1) by incorporating the time-dependent variable  $t_{\text{prop}}$ :

$$P_{\text{new}_i} = P_i \times t_{\text{prop}_i} \quad (2)$$

where  $t_{\text{prop}_i}$  is the proportion of a year that an average individual of species  $i$  spends at a given habitat, and represents the proportion of any fishery landings at a habitat that

has local production.  $P_{\text{new}}$  can be thought of as the local fish production that would likely be lost if the reef was removed, and the local production is entirely new production when  $t_{\text{prop}} = 1$ . The variable  $t_{\text{prop}_i}$  also allows us to estimate the flux of biomass ( $B_{\text{flux}}$ , kg) through a given habitat over the same time frame for species  $i$ :

$$B_{\text{flux}_i} = \frac{B_i}{t_{\text{prop}_i}} \quad (3)$$

$B_{\text{flux}_i}$  is the total biomass of species  $i$  that uses this habitat at any point throughout a year, and tells us about the exchange of biomass in the habitat for a species or an assemblage ( $B_{\text{flux}} = \sum B_{\text{flux}_i}$ ; Table 1). For entirely resident species ( $t_{\text{prop}_i} = 1$ ),  $B_{\text{flux}_i}$  is simply the standing stock biomass that has no exchange. The higher the  $B_{\text{flux}_i}$ , the more the biomass of species  $i$  is potentially exposed to fishing at the habitat. By contrasting the reef's total  $B_{\text{flux}}$  with the reef's total  $B$  ( $\sum B_i$ ), we can observe whether the habitat is used mainly by visitor species (a small  $B/B_{\text{flux}}$ ) or mainly by residents (a large  $B/B_{\text{flux}}$ ). The  $B/B_{\text{flux}}$  ratio is equivalent to a whole-reef  $t_{\text{prop}}$  weighted by biomass and is the proportion of total fish biomass moving through the reef that has local production. When this ratio is small, an artificial reef that is fished could be overexploited.

The parameter  $t_{\text{prop}}$  is essential to this simple approach for refining the understanding of local fish production, and its purpose is akin to that of the 'reef exclusivity index' of

Peterson et al. (2003). The logic behind  $t_{\text{prop}}$  relies on the fact that organisms need habitat to grow and survive, and the proportion of time that an organism uses a particular habitat represents the value of that habitat to its growth and survival. In terms of reef habitats, obligate reef fishes that spend all their time on a given reef will likely disappear if that reef is removed. This process ignores any density-dependent responses in nearby habitats, but the difficulty in accounting for this density dependence is one reason why the production versus attraction debate continues. If a portion of the reef is removed, or an organism spends some of its life elsewhere, then only part of the fish production is likely to disappear. The closer  $t_{\text{prop}}$  gets to 1, the more likely it is that the local area is providing the essential services of food and refuge, and if a species spends all its time using the reef ( $t_{\text{prop}} = 1$ ), then it must be assumed that the species is reef obligate and all its production can be attributed to that habitat. Fish can and do move between habitat sites, so removing one habitat area may not mean all fish production from obligate residents is lost, but  $t_{\text{prop}}$  is likely to correlate with the abundance and quality of nearby alternative habitats that could be used were an area of habitat removed. For example, a reef-resident species found in a mosaic of reef patches is likely to move around and have a smaller  $t_{\text{prop}}$  (for one reef patch) than the same species on a single isolated reef.

### Study area and sampling

We used the approach described above to estimate fish production on a coastal artificial reef off Sydney, Australia (33°50.797'S, 151°17.988'E). The steel reef was deployed in October 2011, is 15 m by 12 and 12 m tall, and sits at a bottom depth of 38 m. The reef has a surface area of ~606 m<sup>2</sup> and volume ~700 m<sup>3</sup>. The reef is further detailed in Scott et al. (2015) and Champion et al. (2015).

To estimate the standing stock biomass for each fish species ( $B_i$ ) on the reef, the density of each species was estimated and then converted to biomass using observed or inferred average body size. Density and body size were estimated using remote visual surveys. Three survey methods were used to estimate fish density: drop cameras (Champion et al. 2015), benthic remote underwater video (RUV; akin to benthic BRUV (Lowry et al. 2012) but without bait), and surveys by a remotely operated vehicle (ROV; Champion et al. 2015). Drop camera surveys were of ~10-min duration and focused on filming the top of the reef. The RUV surveys were of ~40-min duration and focused on filming the base and surrounding benthos of the reef. The ROV surveys were of ~40-min duration and filmed all parts of the reef, including the internal volume. A total of 24 drop camera surveys, 3 RUV surveys, and 3 ROV surveys were done between February 2012 and September

2015, with each survey done on a different day. Sampling days were spread throughout the year to incorporate any seasonal trends in fish abundance (Online Resource 1, Fig S1). For cases where sampling is unevenly distributed across seasons, season-specific mean fish abundances are a prudent option. Generally, the frequency and intensity of sampling should reflect the variability of abundance in a system and the duration over which production estimates are to be applied. Annual production estimates would thus require sampling over at least a year (Warburton 1979; Allen 1982; Cowley and Whitfield 2002), and at seasonal if not monthly intervals (Allen 1982). In a system that is very dynamic, it is realistic to expect that production estimates are relevant over only the same temporal scales as the sampling programme.

The 'reef habitat' surveyed in this study was defined as the volume within the reef and out to 5 m from the reef. This distance was chosen based on information that resident fish that use the reef as refuge forage out to this distance (Champion et al. 2015). The seafloor area under the habitat volume surveyed was 550 m<sup>2</sup>. Fish density (fish m<sup>-3</sup>) was estimated from the video footage by measuring the abundance of each fish species observed on a random selection of still frames from all suitable footage and estimating the volume sampled within each frame (as in Champion et al. 2015). Whole-reef abundance for each species was then estimated by multiplying this density by reef volume. To avoid overestimating species that may only use a certain part of the reef, the reef was divided into five sections that might differ in their association with different functional groups (e.g. benthic, demersal, reef, or pelagic species; Table S3), and total reef abundance for each species was measured as the sum of their section abundances. Abundance was first estimated for species  $i$ , in section  $s$ , on day  $d$  ( $N_{i,s,d}$ ), by averaging the abundances across  $f$  video frames:

$$N_{i,s,d} = \frac{\sum_{f=1}^f D_{i,s,d,f} V_s}{f} \quad (4)$$

where  $D_{i,s,d,f}$  is the fish density (fish m<sup>-3</sup>) in video frame  $f$  and  $V_s$  is the total volume (m<sup>3</sup>) of section  $s$ . This abundance was then averaged across sampling days ( $d$ ) and then summed across all sections ( $s$ ) to get an average whole-reef abundance for each fish species. The number of video frames analysed for each section varied across days and reef sections. A total of 284 frames were analysed.

The whole-reef abundance for each species ( $N_i$ ) was converted to biomass ( $B_i$ ) using average body mass for each species. Body mass was derived from average body length using the standard length–weight relationship (see Online Resource 1). Average body lengths were measured using stereo-BRUV (Harvey and Shortis 1995), which was

**Table 2** Average local production ( $P$ ), new production ( $P_{\text{new}}$ ), and biomass flux ( $B_{\text{flux}}$ ) for species observed on the coastal artificial reef in this study, and total reef values

Common name	$B$ (kg)	$M$ (year <sup>-1</sup> )	$F$ (year <sup>-1</sup> )	$t_{\text{prop}}$	$P$ (kg year <sup>-1</sup> )	$P_{\text{new}}$ (kg year <sup>-1</sup> )	$B_{\text{flux}}$ (kg year <sup>-1</sup> )
1. Yellowtail scad	154.8	0.38	0.25	0.75/365	97.6	0.20	75,336.9
2. Mado	78.4	0.44	0.01	90/365	35.0	8.62	318.0
3. Yellowtail kingfish	78.3	0.40 <sup>c</sup>	0.20	0.5/365	47.0	0.06	57,134.3
4. Silver trevally	18.7	0.60	0.10	2/365	13.1	0.07	3415.8
5. Longfin pike	14.2	0.42	0.05	7/365	6.63	0.13	739.3
6. Ocean leatherjacket	6.60	0.90 <sup>d</sup>	0.20	1/365	7.26	0.02	2408.1
7. Spotted wobbegong	5.57	0.14	0.10	10/365	1.35	0.04	203.3
8. Threebar porcupinefish	4.67	0.34	0	1/365	1.59	0.004	1704.7
9. Grey morwong	3.39	0.22 <sup>e</sup>	0.10	36/365	1.08	0.11	34.3
10. Port Jackson shark	1.02	0.13	0.01	0.82/365	0.15	0.000	454.3
11. Bluestriped goatfish	0.37	0.30	0.05	5.2/365	0.13	0.002	26.0
12. Sixspine leatherjacket	0.27	0.36	0.10	7/365	0.13	0.002	14.31
13. Southern maori wrasse	0.26	0.64	0.05	90/365	0.18	0.04	1.04
14. Stripey	0.23	0.29	0	90/365	0.07	0.02	0.92
15. Crimsonband wrasse	0.19	0.45	0.05	90/365	0.10	0.02	0.78
16. Halfbanded seaperch	0.17	0.39	0	90/365	0.07	0.02	0.71
17. Eastern hulafish	0.01	0.43	0	90/365	0.003	0.001	0.03
18. Old wife	0.01	0.28	0.01	2/365	0.002	0.000	1.50
Total	367.1 <sup>a</sup>				211.3 <sup>b</sup>	9.4	141,794.3

Required parameters are natural mortality ( $M$ ), fishing mortality ( $F$ ), standing stock biomass ( $B$ ), and the proportion of 1 year an individual of a species occupies a specific ( $t_{\text{prop}}$ ; expressed as a fraction in units of days). Species names are given in Online Resource 1 (Table S1).  $t_{\text{prop}}$  values are justified in Online Resource 1 (Table S2)

<sup>a</sup> Equivalent to 668 g m<sup>-2</sup> seafloor, or 606 g m<sup>-2</sup> reef surface area

<sup>b</sup> Equivalent to 384 g m<sup>-2</sup> seafloor year<sup>-1</sup>, or 302 g m<sup>-3</sup> reef year<sup>-1</sup>

<sup>c</sup>  $M$  reduced to match  $Z = 0.6$  (Stewart et al. 2001)

<sup>d</sup>  $M$  reduced to match  $Z = 1.1$  (Miller and Stewart 2009)

<sup>e</sup>  $M$  reduced to match  $Z = 0.32$  (Stewart and Hughes 2009)

deployed 26 times over the sampling period, with each deployment lasting ~30 min. Detailed stereo-BRUV methodology can be found in Online Resource 1. Average body lengths were measured using stereo-BRUV for 15 of the 18 fish species observed during this study, and body lengths for the remaining 3 species were taken as a fixed proportion of maximum length (Online Resource 1, Table S1).

Natural mortality for each species ( $M_i$ ) was estimated using Gislason's second estimator (Kenchington 2013; Online Resource 1). This requires von Bertalanffy growth parameters, which were sourced from the published literature or Fishbase, and also average body lengths for each species (Table S1). Fishing mortality was estimated for those species that form part of the NSW commercial catch and/or are known to be caught recreationally (NSW DPI, personal communication). This was done using the primary literature when available or otherwise inferred. If the sum of  $F_i$  and  $M_i$  exceeded the primary literature estimates of total mortality ( $Z_i$ ) for a species, then the literature value of  $Z_i$  was used instead. The parameter  $t_{\text{prop}}$  is difficult to

estimate, but is done so most effectively with telemetry or tagging studies. In this article,  $t_{\text{prop}}$  is inferred based on telemetry, visual observations, and species life history (Table S2).

## Results and discussion

### Fish biomass and production at the artificial reef

The measured average standing stock biomass  $B$  at this artificial reef was large, at ~370 kg within 5 m of the reef (Table 2). This reef has substantially less submerged surface area per unit seafloor (~3.4 m<sup>2</sup> m<sup>-2</sup>) than the taller oil platforms in Claisse et al. (2014) (~11.8 m<sup>2</sup> m<sup>-2</sup>), but has a larger fish biomass density (668 g m<sup>-2</sup> seafloor, compared to 514 g m<sup>-2</sup> in Claisse et al. 2014). This biomass is similar to the average biomass across a range of artificial reefs and materials including designed concrete reefs of 650 g m<sup>-2</sup> (Stone et al. 1979; Polovina 1991), and more

than reefs made from tires ( $68\text{--}218\text{ g m}^{-2}$ ) or car bodies ( $26\text{--}166\text{ g m}^{-2}$ ). This biomass also exceeded surveyed tropical natural reefs  $27\text{--}158\text{ g m}^{-2}$  (Stone et al. 1979) or  $100\text{--}500\text{ g m}^{-2}$  (Stevenson et al. 2007), and the average biomass of fish on a range of fished and unfished temperate and tropical shallow reefs  $122\text{ g m}^{-2}$  (Edgar and Stuart-Smith 2014; Edgar et al. 2014).

Our modelling shows that local production  $P$  at this reef is also large, at  $211\text{ kg year}^{-1}$  (Table 2). This value is equivalent to  $\sim 380\text{ g m}^{-2}$  of seafloor  $\text{year}^{-1}$ , well within the  $105\text{--}887\text{ g m}^{-2}\text{ year}^{-1}$  range reported for oil platforms, and exceeds production at surveyed natural habitats (Polovina 1991; Claisse et al. 2014). Restored oyster reefs may produce  $\sim 190\text{ g fish m}^{-2}\text{ year}^{-1}$  (Peterson et al. 2003), and fished concrete artificial reefs possibly  $\sim 280\text{--}440\text{ g fish m}^{-2}\text{ year}^{-1}$  (Powers et al. 2003). Due to the study's design, the latter result cannot be attributed to a specific reef, and their method for calculating production may be more generous than ours by including the off-reef production of 'recruitment-enhanced' fish (Peterson et al. 2003). It does appear certain that designed or modified habitats can be extremely productive. The large fish production on the reef in this study can be attributed to its high complexity, its exposure to ocean currents that provide enormous planktonic food production (Champion et al. 2015), and the association of schooling species like yellowtail scad and kingfish (Scott et al. 2015). This local production  $P$  approximates the biomass that can be extracted each year without the landings 'footprint' exceeding the boundaries of the reef habitat.

It is likely that our estimates of biomass and production are inflated relative to the oil platforms in Claisse et al. (2014). Claisse et al. only counted fish within 2 m of the reef itself, while we chose 5 m. Claisse et al. did not count highly mobile species (such as the yellowtail scad or kingfish in this study), which we did. If these visitor species are removed from our analysis, fish production at our reef declines to  $121\text{ g m}^{-2}\text{ year}^{-1}$  which is still within the range reported for oil platforms. We think it is essential to include these visitors because they are important reef-associated species, but we stress that rigorous monitoring must be done to ensure the estimates of standing stock biomass are reliable for these often patchy species. So although it appears our artificial reef is as productive as oil platforms, it is likely that the production values reported by Claisse et al. (2014) are conservative and likely to exceed the production on the smaller, albeit still large and complex, designed artificial reefs such as the one in this study.

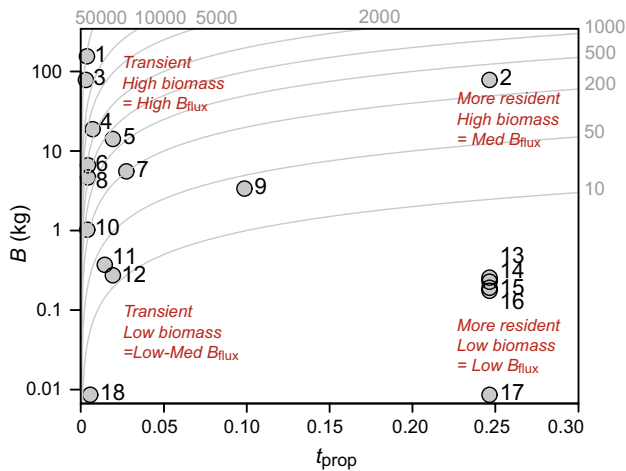
### New fish production

Not all of the local fish production was likely to be 'new'. The production modelled was certainly local production

and would largely vanish from that specific location if the reef was removed, but this does not mean it was new production. New production  $P_{\text{new}}$  is the production that would disappear from the ecosystem (not just the location) if the reef was removed. Our estimates of  $t_{\text{prop}}$  resulted in a total  $P_{\text{new}}$  value of  $9.4\text{ kg year}^{-1}$  (or  $17\text{ g m}^{-2}\text{ year}^{-1}$ ), which is 4.4 % of the total local production (Table 2). Almost all of  $P_{\text{new}}$  was due to the resident reef zooplanktivore mado, which is a highly reef-associated and productive species on this reef (Champion et al. 2015). Claisse et al. (2014) excluded transient visitors from their study, and the *Sebastes* species that provided much of the production on oil platforms can show strong residency (*Sebastes* spp.: Carlson and Haight 1972; Mitamura et al. 2009). This means that the local production values of Claisse et al. are likely to include a larger proportion of new production than our study's 4.4 %. The use of an 'index of reef exclusivity' term in the studies of Peterson et al. (2003) and Powers et al. (2003), which acknowledges the range of species-specific affinities of fish with reef, attempts to distinguish between new and 'aggregated' production. This index is based on the diets of associated fish species and is often quite high ( $\sim 0.75$ ). We feel this index does not accurately estimate new production, which requires insight into spatial/temporal association of these fish with the reef and surrounding habitats. Thus, their production estimates are likely to be much closer to local production than new production. An attempt at partitioning new and local production was done by Polovina (1991) who inferred new production may be  $\sim 1\%$  of local production.

### The flux of biomass across the reef

The use of  $t_{\text{prop}}$  (the average proportion of a year that an individual of a species occupies a habitat) also allows us to estimate the amount of fish biomass that passes through the defined artificial reef habitat each year ( $B_{\text{flux}}$ ). This was  $\sim 142$  tonnes of fish per year (Table 2) and is much (but probably not all) of the fish biomass that is exposed to fishing at this reef. The  $B/B_{\text{flux}}$  ratio (which approaches 1 as all species become resident) was 0.0026, meaning that only  $\sim 0.26\%$  of the biomass that passes through the habitat has local reef-associated production. This means that this artificial reef is a great place to catch fish without locally depleting the fish biomass, but this is also a situation that can lead to unsustainable fishing. The range of  $B$  and  $t_{\text{prop}}$  values observed across species (Fig. 1) reveals that these whole-reef patterns are driven largely by 2–3 species, and the yellowtail scad and kingfish alone accounted for 93 % of  $B_{\text{flux}}$ . The  $B/B_{\text{flux}}$  ratio is a useful metric for understanding the effects of artificial reefs on the movement and distribution of fish biomass, and gets at the heart of the 'production–attraction' debate. Reefs that have a large flux of



**Fig. 1** A biplot of the steady-state biomass ( $B$ , kg) and estimated  $t_{\text{prop}}$  (the average proportion of a year that an individual of a species occupies a habitat) for the fish species in this study. Numbers refer to species numbers in Table 2; grey lines and numbers indicate  $B_{\text{flux}}$ . Note that the y-axis is log-scaled. The species observed in this study varied in biomass and residency and thus in biomass flux. It is when  $B_{\text{flux}}$  greatly exceeds  $B$  (i.e. small  $t_{\text{prop}}$ ) that a species is at risk of overexploitation at the spatial scale of the reef

associated biomass and relatively low local production could be defined as reefs vulnerable to overexploitation. This is our interpretation of the ‘production versus attraction’ debate—that vulnerable reefs are those typically driven by attraction—but our approach shows that they are vulnerable not because they have an highly associated fish biomass that gains no benefit from the reef (which we feel is unlikely) but because there is a high flux of loosely associated biomass. We do not suggest that this pattern of high biomass flux is unnatural or unique to artificial reefs. It is likely that many habitats, natural or otherwise, show great variation in biomass flux, and measuring this flux can elucidate the effects that modifying habitats may have on the biota that use them. Fish aggregating devices (FADs), for example, offer a variety of benefits to fish (Castro et al. 2002) but are used predominantly by transient visitor species (Girard et al. 2004; Dempster 2005; Folpp and Lowry 2006). Thus, FADs would be expected to have a very small  $B/B_{\text{flux}}$  ratio. The method detailed here for estimating production on reefs could equally be used for FADs to quantify their relative potential for overexploitation.

## Conclusion

This study presents a new approach to understanding the dynamic nature of habitat associations of fish, with a specific goal to develop a simple numerical model addressing the production versus attraction issue for artificial

reefs. This approach showed that a designed artificial reef can be extremely productive and comparable to oil platforms as some of the most productive marine fish habitats. This result could be expected given that these reefs have features (i.e. shape, complexity, location) specifically designed to promote fish production (as opposed to ‘opportunistic’ habitats such as oil rigs). Only a fraction (4–5 %) of the local fish production was likely to be new, however, and this could be reduced if processes such as density-dependent habitat selection or predator–prey responses that occur outside the ecological and spatial boundaries of this artificial reef were considered. This reef was found to have a small  $B/B_{\text{flux}}$  ratio, indicating a large abundance of associated visitor species and the reef’s susceptibility to overexploitation from fishing. The success of an artificial reef depends on its specific objectives, but a reef with a large  $B/B_{\text{flux}}$  ratio (which indicates a more resident fish assemblage) is more likely to encourage sustainable fishing due to the comparative ease of linking fishing landings with local fish production. However, if fished artificial reefs are well managed and fishing harvest rates across a broader area are sustainable, then artificial reefs with small  $B/B_{\text{flux}}$  ratios (i.e. more transient fish assemblages) can still be successful as highly productive yet sustainable marine habitats.

**Acknowledgments** We are grateful to Stephanie Brodie and Krystle Keller for sharing telemetry data. This research was funded by an Australian Research Council Linkage Project (LP120100592). This article is Sydney Institute of Marine Science Contribution #185. All fish observations were carried out ethically, and no biota were collected.

**Funding** This research was funded by an Australian Research Council Linkage Project (LP120100592).

## Compliance with ethical standards

**Conflict of interest** All authors declared that they have no conflict of interest.

**Ethical approval** This research was done under University of NSW Animal Care and Ethics Committee (ACEC) approval #10/15B.

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