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Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches

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Two widely-recognized hypotheses propose that increases in fish abundance at artificial reefs are caused by (a) the attraction and redistribution of existing individuals, with no net increase in overall abundance and (b) the addition of new individuals by production, leading to a net increase in overall abundance. Inappropriate experimental designs have prevented many studies from discriminating between the two processes. Eight of 11 experiments comparing fish abundances on artificial reefs with those on adjacent soft bottom habitats were compromised by a lack of replication or spatial interspersion in the design itself. Only three studies featured proper controls and replicated designs with the interspersion of reef and control sites. Goodness of fit tests of abundance data for 67 species from these studies indicated that more fishes occur on reefs than on controls, particularly for species that typically occur over hard substrata. Conversely, seagrass specialists favour controls over reefs. Changes in the appearance of fish abundance trajectories driven by manipulation of sampling intervals highlight the need for adequate temporal sampling to encompass key life history events, particularly juvenile settlement. To ultimately determine whether attraction and production is responsible for increased abundances on reefs, requires two experimental features: 1) control sites, both interspersed among artificial reefs and at reef and non-reef locations outside the test area and 2) incorporation of fish age and length data over time. Techniques such as otolith microchemistry, telemetry and stable isotope analysis can be used to help resolve feeding and movement mechanisms driving attraction and production.

Keywords: artificial reef; chemical tracers; experimental design; meta-analysis; tracking techniques.

INTRODUCTION

Over the past century, various structures (*e.g.* car bodies, scrap tyres, pulverized ash blocks and wrecks) have been deployed as artificial reefs to increase the abundance of commercially and recreationally important fish species. Scientific research into artificial reefs has gathered pace internationally since the 1950s, with artificial reefs throughout South East Asia, the Mediterranean Sea, the Middle East, the Caribbean, California, South America and Australia (see Table I).

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TABLE I. Examples of artificial reefs in the literature from 1984 to 2004

Study	Location	Reef material	Duration	Questions posed by study/Purpose of study
Alevizon *et al.* (1985)	Deep Water Cay, Bahamas	PVC pipe and concrete blocks	12 months	Does the size and position of a reef influence population growth and eventual community structure?
Pollard & Matthews (1985)	Australia and New Zealand	Tyres, vessels, concrete, composite structures	Variable	Analyses Australian literature on reefs and FADs between 1965 and 1984.
Alevizon & Gorham (1989)*	Looe Key, Florida, U.S.A.	PVC pipe and concrete blocks	24 months	Does the deployment of artificial reefs affect resident fish communities of adjacent reefs and reef-associated habitat?
DeMartini *et al.* (1989)	San Diego, California, U.S.A.	Quarry rockpiles	3 months	Compares and contrasts patterns of fish density and abundance at an artificial reef and adjacent rocky-bottom kelp forest.
Polovina & Sakai (1989)	Shimamaki, Japan	Cylindrical concrete modules of variable size	20 years	Quantifies extent to which reefs produce sustainable increases in fishery production by analyses of annual catch and catch per unit effort values.
Spanier *et al.* (1990)	Haifa, Israel	Tyres, concrete, polypropylene rope, wire, chain	4 years	Can artificial reefs solve problems associated with limited habitat and food resources in oligotrophic waters?
Bohnsack *et al.* (1994)*	Miami Keys, Florida, U.S.A.	Concrete modules	20 months	(1) Does reef size affect colonisation and (2) Are observed increases in fish abundance due to settlement of new recruits or redistribution from elsewhere?
Bombace *et al.* (1994)	Adriatic Sea, Italy	Concrete blocks of variable size and arrangement	4 years	Evaluates (1) influence of artificial reefs on fish assemblages, (2) suitability of reefs for epibenthos and (3) influence of surrounding habitat on 'reef effect'.
Bortone *et al.* (1994)	Choctawhatchee Bay, Florida, U.S.A.	Polyolefin plastic cones	12 months	Are modular reefs suitable for the management of target species? Also identifies reef properties associated with increases in fish abundance.
Branden *et al.* (1994)	Australia	Motor vehicle tyres, derelict vessels	7 years	Reviews artificial reef developments in Australia between 1984 and 1991
Chua & Chou (1994)	Palua Hantu, Singapore	Concrete blocks, tyre pyramids	18 months	Can reefs increase the productivity of denuded and barren seafloor areas?
D'Anna *et al.* (1994)*	Sicily, Italy	Concrete blocks of variable size and arrangement	12 months	Compares community structure of an artificial reef with surrounding habitat.
Fabi & Fiorentini (1994)*	Adriatic Sea, Italy	Concrete blocks of variable size and arrangement	4 years	Compares assemblages at reef and control sites, evaluates impact of reef on fishing yield and compares catch data with visual observations.
Johnson *et al.* (1994)	San Diego, California, U.S.A.	Quarry boulders	7 months	Estimates (1) fish production, (2) food resources and (3) fidelity for reef residents and those associated with adjacent sand bottom.
Kim *et al.* (1994)	South Korea	Concrete blocks of variable size and arrangement	5 years	Do artificial reef structures affect community composition and abundance?
McGlennon & Branden (1994)*	Adelaide, South Australia	Tyre tetrahedrons	12 months	Quantifies and compares fishing effort, catch rates and catch compositions derived from artificial reefs and surrounding natural seabed habitat.

Fujita *et al.* (1996)*	Iwate, Japan	Concrete and polyethylene-concrete blocks	6 years	Quantifies differences between and seasonal variation within artificial reef, natural reef and sand-mud bottom communities.
Santos & Montiero (1997, 1998)*	Olhao, Portugal	Concrete blocks of variable size and arrangement	4·5 years	Can artificial reefs (1) affect community structure, (2) raise the nursery effect of a lagoon and (3) affect fishing yield?
Rilov & Benayahu (1998)	Eilat, Israel	Steel pillars with and without barb-wire enclosure	9 months	Can vertical pillars supporting oil jetties serve as a model for the construction of new artificial reefs in the Middle East?
Vose & Nelson (1998)	Vero Beach, Florida, U.S.A.	Concrete blocks, stabilized coal and oil ash blocks	27 months	Do fish utilize coal and oil ash reefs similarly to concrete reefs?
Clark & Edwards (1999)*	Galu Falhu, Maldives	Hollow concrete blocks, concrete Mattresses, chain-link fencing	3·5 years	Evaluates four artificial reef materials as tools for marine habitat rehabilitation in terms of coral and fish colonization.
Golani & Diamant (1999)	Gulf of Elat, Israel	Disused vehicles and construction construction equipment	24 months	Monitors patterns of fish colonization onto new artificial reefs.
Heise & Bortone (1999)*	Choctawhatchee Bay, Florida, U.S.A.	Plastic crates and concrete tiles	12 months	Can artificial reefs be used to encourage seagrass growth?
Sherman *et al.* (1999)	Fort Lauderdale, Florida, U.S.A.	Reef ball (TM) modules	19 months	Does fish recruitment and aggregation to artificial reefs vary with depth?
Sanchez-Jerez & Ramos-Espla (2000)*	Alicante, Spain	Concrete blocks of variable size and arrangement	34 months	Does the deployment of anti-trawling reefs in seagrass meadows lead to changes in fish assemblage structure?
Jebreen (2001)	Queensland, Australia	Disused vehicles and vessels, tyres, pipes, rubble	3–30 years	Reviews literature on reef effect on fish stocks, analyses survey data from Queensland reefs, evaluates design and construction aspects of reef materials.
Zalmon *et al.* (2002)	Rio de Janeiro, Brazil	Concrete blocks, tyres	24 months	Do artificial reefs have an effect on local fish assemblages and do they lead to increased fishing yield?
Perkol-Finkel & Benayahu (2004)	Eilat, Israel	Vertical metal and PVC nets	7 months	Compares community structure of stony and soft corals on vertical unplanned artificial reefs and existing natural reefs.

* those including explicit reef *v.* control fish abundance comparisons.

Most research to date has recorded significant post-deployment increases in fish abundance on and around reefs, concurrent with increases in the benthic organisms that fishes may consume (Pickering & Whitmarsh, 1997; Glasby, 1999; Sanchez-Jerez & Ramos-Espla, 2000). Many mechanisms may be responsible for these increases, but their importance has rarely been evaluated. Consequently, the results reported and conclusions drawn from previous artificial reef studies are the subject of an ongoing 'attraction *v.* production' debate (Bohnsack *et al.*, 1997; Pickering & Whitmarsh, 1997; Bortone, 1998).

ATTRACTION *V.* PRODUCTION HYPOTHESES

The attraction *v.* production debate gained momentum following the International Artificial Reef Conference of 1983, when fisheries scientists challenged the former assumption of habitat limitation on population size for reef species (Bohnsack *et al.*, 1997; Lindberg, 1997), *i.e.* that the amount of hard-bottom habitat available did not necessarily restrict the distribution and abundance of species. The argument was that while stocks of reef species had been heavily exploited to low levels, the amount of reef habitat available had remained the same, still able to support greater numbers. Consequently, reef habitat could not be regarded as the primary factor restricting fish populations and addition of artificial reefs was assumed to be of no benefit. Increases in fish density around reefs, however, were apparently more common than decreases in density, so an explanation was still required.

Two opposing, yet not mutually exclusive models have been proposed to explain increased abundances. The attraction hypothesis suggests that artificial reefs simply attract fishes from surrounding habitat as a consequence of fish behaviour (Bohnsack, 1989). The reefs act purely as fish aggregation devices (FADs), providing behavioural cues that exploit the thigmotactic tendencies of fish species (*i.e.* their tendency to move towards structured rather than bare, featureless habitat). Fishes moving onto artificial reefs are unable to be replaced due to limits on the abundance of fishes in the area (*e.g.* finite larval or food supply). Thus reefs do not significantly increase local populations. The apparent increase in abundance following reef deployment may be short-term in cases where local fishing activity targets reefs soon after deployment. The reefs concentrate existing individuals into a smaller area of habitat, making segments of fish stocks that may have been previously unavailable or cost-ineffective to exploit more vulnerable (Grossman *et al.*, 1997) by increasing the efficiency of fishing activity. This may permit rapid exploitation of populations, potentially to the point of collapse. Apart from simple thigmotaxis, mechanisms behind attraction may include (a) increased feeding opportunities and (b) increased shelter from predators.

Alternatively, the production hypothesis proposes a more positive outcome. Rather than concentrating existing individuals into a smaller area, artificial reefs provide additional habitat, increasing an area's carrying capacity (Bohnsack, 1989). As is the case with attraction, increased feeding and shelter opportunities encourage fishes to settle at reefs, but a greater number of juveniles are able to settle, survive to spawn as adults and contribute new individuals to local

populations. The reef promotes a net increase in local abundance of fishes because new individuals can be accommodated by new (*i.e.* artificial reef) habitat.

The degree of attraction or production following reef deployment will depend on the characteristics of surrounding habitat, particularly in terms of spatial heterogeneity and nutrient availability. For example, attraction is more likely where a single reef is introduced into an oligotrophic environment. Production will be more likely with the addition of more reefs, or more complex reefs. The degree of attraction and production will also be influenced by management protocols, *e.g.* whether reefs are deployed into no-take reserves or zones where fishing is unregulated.

LIMITATIONS OF PREVIOUS STUDIES

Few studies comparing fish abundance on artificial reefs with natural habitat have attempted to evaluate the relative significance of attraction and production. Longitudinal data, which are required to (a) determine the length of association of individuals recruiting to artificial reefs, (b) determine the growth and survival pattern of those recruits, (c) isolate whether production arising from those recruits exceeds that of neighbouring non-reef populations and (d) assess the relative contributions of attraction and production as mechanisms driving increases in fish abundance, have rarely been collected. The use of such data in resolving attraction *v.* production is complicated by the high mobility of some reef species (Vose & Nelson, 1998; Fowler *et al.*, 1999) and uncertainties regarding species-specific variables such as diet, behaviour, age-specific growth and mortality rates. All of these variables change under the divergent scenarios of attraction and production, with or without background fishing pressure (Powers *et al.*, 2003). There is also a lack of experimental data in the literature addressing: (a) how differences in reef design affect fish abundance, (b) the influence of reef location (with regard to larval supply, background spatial heterogeneity and trophic status) on fish assemblages and (c) the transfer of biomass from producers to consumers. The lack of biomass transfer data reflects a simplistic focus on changes in abundance alone, rather than investigation of trophic events and links that could be driving those changes. Recent advances in the use of chemical tracers and tracking techniques provide novel tools potentially able to help resolve the attraction or production debate.

ADDRESSING KNOWLEDGE GAPS: DESIGN, SCALES OF DEPLOYMENT, APPROPRIATE SAMPLING SCHEMES AND TROPHIC CONSIDERATIONS

Fishes remain on and around reefs for variable periods, depending on their age and taxonomy and the characteristics and location of the reefs (Bohnsack & Sutherland, 1985). Ultimately, the desirable outcome for artificial reef deployment is successful maintenance of or increase in abundance of target species by increased production instead of potential reduction *via* attraction. Reef design (Shulman, 1984; Hixon & Beets, 1989; Omar *et al.*, 1994; Pondella & Stephens, 1994; West *et al.*, 1994; Gregg, 1995) and location (Dean, 1983; Frazer &

Lindberg, 1994) can both affect the final outcome regardless of the status of local fish populations and existing habitat prior to deployment. The potential benefits of artificial reefs can be maximized by considering the biology and behaviour of target species during the reef design process (Seaman *et al.*, 1989). The scale of deployment and the timing and interval of sampling, however, are factors that are particularly important in determining whether increased abundance is attributable to attraction or production. Consideration of prevailing trophic conditions, spatial heterogeneity (or otherwise), migration of fishes and assessment of biomass transfer from producers to consumers on and around reefs could also lead towards more convincing isolation of mechanisms driving attractive and productive changes in fish abundance.

DESIGN

Design can have a major effect on the capacity of a reef to promote increased fish abundance. Design is more often focused on structural integrity, however, than on catering for individual species and age cohorts in a particular environment (Bohnsack *et al.*, 1994; Gregg, 1995).

Cylindrical structures featuring lateral holes support the highest species diversity, which may be due to the provision of hiding spaces, hollow interior spaces, regions of shadow, high surface area and protrusions (Pickering & Whitmarsh, 1997). Fishes appear to display a preference for cavities similar to their body size (Shulman, 1984; Hixon & Beets, 1989). Reefs without cavities therefore cater more for adults than juveniles, leading to elevated mortality rates following recruitment (West *et al.*, 1994). Variations in vertical relief of reefs will also cater for diverse species requirements by encouraging variable water flow, turbulence patterns, sedimentation regimes and light levels (Pickering & Whitmarsh, 1997).

The degree of attraction and production generated by a design will vary with environmental conditions. For example, reefs of identical design placed close to existing natural and anthropogenic structures exposed to variable currents (*i.e.* a spatially heterogeneous environment) will generate different results to those placed on flat, featureless sand and mud bottoms in areas receiving regular currents (*i.e.* a spatially homogeneous environment).

SCALES OF DEPLOYMENT

The temporal and spatial scale of sampling is an important consideration for separation of reef effects from background variability (Bohnsack *et al.*, 1997). While some studies have examined how the distribution of reefs relates to habitat use and development of prey resources for resident species, few have explicitly attempted to isolate reef effects. Absence of background pre-deployment data (Clark & Edwards, 1999), erroneous and inappropriate experimental design (Alevizon & Gorham, 1989) and infrequent sampling, *e.g.* only once per season (Santos & Monteiro, 1998) have also cast doubt over recorded changes in fish abundances.

One notable exception studied the impact of artificial reefs on production of Pacific giant octopus *Octopus dofleini* (Wülker) and several species of flatfishes in

Japanese waters (Polovina & Sakai, 1989). The authors analysed 30 years of annual catch and catch per unit effort (CPUE) data to quantify the extent to which reefs increased production in two adjacent fishing grounds. Analysis of separate grounds permitted separation of the effect of reefs on catches from other potentially confounding effects such as cohort strength and changes in fishing effort. The annual catch rate of *O. dofleini* increased by 4%. In contrast, catch rates of flatfishes were highly variable but did not increase, implying aggregation or attraction.

In addition to the absence of background pre-deployment data and infrequent sampling of reef structures, spatial confounding of reef and control sites through segregation instead of interspersion (Underwood, 1990) has also cast doubt over recorded changes in fish abundances. Lack of true replication is a common problem in the design of ecological field experiments (Hulbert, 1984). Replication is either at the wrong level (pseudo-replication) or too low to provide enough statistical power for testing hypotheses. The construction, deployment and monitoring of large numbers of artificial reefs can become prohibitively expensive (Parsons, 1982), thus hampering replication. Artificial reefs have usually been designed to cover large areas with base units that are costly to manufacture and deploy (Chua & Chou, 1994; Fujita *et al.*, 1996; Santos & Monteiro, 1997, 1998; Clark & Edwards, 1999). Research generally has not evaluated the use of reefs constructed from relatively cheap materials, whose cost would in turn allow sufficient replication for statistically powerful testing of hypotheses investigating fish abundance changes.

APPROPRIATE SAMPLING FREQUENCIES

In studies with frequent sampling, high variability in abundances of individual species is evidence of key events such as settlement, migration and mortality (Sanchez-Jerez & Ramos-Espla, 2000). The same experimental design sampled at less frequent intervals will fail to detect these events, which are fundamental to distinguishing between attraction and production.

Artificial reefs and controls should be visited at intervals relevant to life history events, *e.g.* every 1–2 months to permit comparisons between and within seasons and detect abundance changes related to recruitment and mortality.

JUVENILE AND ADULT COHORT ANALYSIS

To determine life history events driving peaks and troughs, it is important to distinguish between the contributions of adults and juveniles. For example, large numbers of juveniles may signify postlarval settlement, when juveniles are able to settle and survive upon reefs, due to habitat opportunities offered by them. Adult and juvenile contributions and movements may be distinguished using visual census techniques, tagging, telemetry and destructive sampling for otolith microchemistry and growth ring counting. The last permits construction of age-length frequency distributions (Bohnsack & Harper, 1988) and age-length plots through time. Otolith microchemistry (Campana *et al.*, 1995) can be used to explore prior movements of individuals by analysis of changes in the elemental composition of different parts of otoliths (these reflect environmental conditions,

especially water chemistry). These patterns in movement can be related to observed changes in somatic growth rates implied by growth ring patterns. Knowledge of the abundance, survivorship, movement and somatic growth of individuals within and between age classes helps to distinguish between attraction and production. Tracking fish movement through telemetry and tagging can determine the degree of reef fidelity. Age-length frequency analyses can assist in discriminating between recruitment of new juveniles to reefs and existing adults.

TROPHIC CONSIDERATIONS

One benefit that artificial reefs provide to fishes is additional surface area for the development of encrusting epibenthic assemblages that can provide food for residents (Rezak *et al.*, 1990; Johnson *et al.*, 1994). Reefs have also been implicated in the increased survival of juvenile fishes (Pondella & Stephens, 1994). It may be possible for juveniles to recruit onto artificial reefs in areas outside prior niche boundaries by capitalising on the newly provided food sources. Length and mass conversions (Bohnsack and Harper, 1988), together with gut content (Lindquist *et al.*, 1994) and stable isotope (Peterson, 1999) analyses may be useful for establishing dietary links between fish cohort growth and epibenthic resources on reefs. The use of chemical tracers such as stable isotope ratios in tracking biomass transfer from reef producers to fishes is dependent on the ability to uniquely identify reef producers isotopically. This may be possible through either the presence of producer groups distinct from those in adjacent habitats, or through artificially labelling reef producers with particular isotopes (Winning *et al.*, 1999). The latter approach is considered to be challenging in open marine systems as any labelling effects would be short-lived. The use of construction material that naturally leaches specific chemicals into the reef producer biomass may provide tracers that will indicate fish dependence on reef producers.

The transfer of consumer biomass (*i.e.* epibenthos) to producers (*i.e.* recruits) may be critically important in the survival of fishes at reefs. Unfortunately, previous studies have tended to focus on changes in fish numbers alone without investigating trophic transfer. Demonstrating conversion of reef epibenthos into fish biomass is an important step towards attributing increased fish abundance to attraction or production.

A META-ANALYSIS OF 'USEFUL' STUDIES

The focus of this paper is research investigating the effects of deploying artificial reefs into areas of soft bottom habitat. All studies published between 1984 and 2004 which compared fish abundances at sub-tidal artificial reefs with surrounding soft bottom habitat using an experimental approach were examined. Although comparisons between artificial reefs and natural reefs are of interest ecologically (Carr & Hixon, 1997), such comparisons were excluded from consideration in the meta-analysis. Many artificial reef studies reviewed were descriptive, correlative and comparative and investigated many valid hypotheses (Table I), however, few studies fulfilled the basic requirements for a

proper experimental design (*i.e.* controls, treatments, replication and interspersion).

The most recent artificial reef review (Peterson *et al.*, 2003) synthesized results from eight studies to estimate enhancement of production on restored oyster reefs. The majority of studies in Peterson *et al.* (2003) featured suitable controls, however, they were excluded from further consideration in the current review because they were: (a) based upon restored, existing biogenic reefs rather than new anthropogenic reefs, (b) were mostly inter-tidal or (c) results were not reported in peer-reviewed literature.

Of the 11 studies isolated that featured explicit comparisons between sub-tidal artificial reefs and adjacent sub-tidal soft-bottom habitat controls (Table I), eight were compromised by a lack of replication. The remaining three studies (Bohnsack *et al.*, 1994; McGlennon & Branden, 1994; Sanchez-Jerez & Ramos-Espla, 2000) featured designs incorporating sufficient replication and interspersion of reefs and controls and were used in the meta-analysis.

META-ANALYSIS METHODS & RESULTS

Results for 67 fish species combined across all three aforementioned studies were included in the meta-analysis. Species were excluded where catch rates were low (*e.g.* <20 individuals across both reefs and controls). Each of the 67 species was assigned to one of three results classes: (a) species displaying significantly greater abundance on reefs than on controls, (b) species displaying abundances on reefs and controls that were not significantly different and (c) species displaying significantly greater abundance on controls than on reefs.

Class assignments for species encountered by Bohnsack *et al.* (1994) were based upon differences in the importance percentage (based on abundance, biomass and frequency) of species across reef and controls. Class assignments for species encountered by McGlennon & Branden (1994) were based upon differences between mean catch rates of species across reefs and controls. Class assignments for species encountered by Sanchez-Jerez & Ramos-Espla (2000) were based upon two techniques: one based upon statistical manipulation of reported mean abundance results (which incorporated S.E. indicative of seasonal variation) using two-tailed *t*-tests and another based upon the raw percentage difference between reported mean values (*e.g.* were mean values > 5% apart?).

Following class assignment, two χ^2 tests were conducted based on an expected 1 : 1 : 1 ratio (*i.e.* no apparent reef effect). The first test included class assignments for species from Sanchez-Jerez & Ramos-Espla (2000) based upon *t*-test results, while the second included class assignments for species from Sanchez-Jerez & Ramos-Espla (2000) based upon raw percentage differences. On both occasions the data did not conform to the 1 : 1 : 1 ratio. In the first test, most (55 of 67) species were either more abundant on reefs (28) or equally abundant on reefs and controls (27) (χ^2, $n = 67$, d.f. = 2, $P = 0{\cdot}027$). The bias towards greater abundance on reefs increased when raw percentage difference results from Sanchez-Jerez & Ramos-Espla (2000) were considered instead of the *t*-test results. Under this situation, 20 of 27 species that were equally abundant on reefs and controls based on *t*-test results were equally redistributed to the

'greater abundance on controls' (12 to 22) and 'greater abundance on reefs' (28 to 38) result classes (χ^2, $n = 67$, d.f. $= 2$, $P < 0{\cdot}001$).

A variety of sources (Kuiter, 1996; Allen, 1997; Froese & Pauly, 2005) were used to assign species groups *a priori* for the characteristics of substratum preference (soft bottom, soft and hard bottom and hard bottom), vegetation association (seagrass, seagrass and algae and algae), reproductive guild (non-guarding egg scatterer and other), feeding guild (herbivory, carnivory and omnivory), vertical distribution (pelagic and benthic), horizontal distribution (inner coastal, mid-neritic and outer-oceanic) and social tendency (gregarious, solitary and mixed). Contingency χ^2 tests were also conducted for these ecological and life history characteristics.

Trends were evident with respect to substratum preference and vegetation association. Most species known to prefer hard substratum (12 of 18, *e.g.* surgeonfishes, *Acanthurus* spp.) displayed greater abundance on reefs, while most species known to prefer soft substratum [17 of 20, *e.g.* blue runner, *Caranx crysos* (Mitchill)] displayed equivalent (11) or greater (6) abundance on controls (χ^2, $n = 61$, d.f. $= 4$, $P = 0{\cdot}011$). Substratum preference was unknown for six species. The strength of both apparent biases was greater when raw percentage difference results from Sanchez-Jerez & Ramos-Espla (2000) were considered (χ^2, $n = 61$, d.f. $= 4$, $P < 0{\cdot}001$). Under this situation, six hard substratum species and seven soft substratum species that had displayed equal abundance on reefs and controls based on *t*-test results were redistributed to the 'greater abundance on reefs' (12 to 18) and 'greater abundance on controls' (6 to 13) result classes.

Almost all species associated with seagrass (27 of 32), *e.g.* blue weed whiting, *Haletta semifasciatus* (Valenciennes) displayed equivalent (20) or greater (7) abundance on controls while most non-seagrass specialists (8 of 12), *e.g.* comber *Serranus cabrilla* (L.) displayed greater abundance on reefs (χ^2, $n = 44$, d.f. $= 2$, $P = 0{\cdot}002$). Vegetation association was unknown for 23 species. The strength of the apparent bias displayed by seagrass species was even greater when raw percentage difference results from Sanchez-Jerez & Ramos-Espla (2000) were considered (χ^2, $n = 44$, d.f. $= 4$, $P = 0{\cdot}014$). These results are not surprising given that seagrasses thrive in areas of soft-bottom substratum under suitable environmental conditions while non-seagrass macrophytes (*e.g.* algae) are characteristically associated with hard substratum.

FURTHER CONSIDERATIONS FOR ARTIFICIAL REEF RESEARCH

Ecology and life history patterns are important in driving the response of fishes presented with a choice between artificial reef and soft bottom habitat. These patterns are so diverse that analysis of the response of entire assemblages to reef *v.* control situations is difficult; therefore a 'case-by-case' approach for individual species or functional groups is preferable. While it is generally accepted that artificial reefs increase local abundance of fishes following deployment (Pickering & Whitmarsh, 1997), mechanisms behind the increase have not been satisfactorily identified. Sampling protocols are complicated by behavioural

responses of fishes to changing light, tides and seasons throughout their life history.

DIEL BEHAVIOUR

Zooplanktonic prey of fishes often exhibit vertical diel migration where individuals ascend during the night to feed at the surface, then descend into deeper waters during the day (Ohman, 1990). Many fishes also exhibit vertical diel migration, possibly for predatory activities (Stich & Lampert, 1981). To minimize the impact of diel behaviour on fish abundance recordings, sampling should be conducted during the day and perhaps even confined to a few hours either side of midday.

TIDAL FLUCTUATIONS

In addition to changing light, fish species may respond to tidal fluctuations. Alterations in the speed and direction of currents can produce pronounced gradients in salinity, temperature and turbidity in the water column. Reducing the impact of this factor in conjunction with light may be possible if sampling is conducted across daylight hours during neap tides when the amplitude of tidal fluctuations is minimized.

SPECIES-SPECIFIC MIGRATIONS

Many species undertake migrations related to their life history, *e.g.* yellowfin bream *Acanthopagrus australis* (Owen) (Griffiths, 2001). Many species have a pattern of offshore migration of adults for spawning followed by inshore settlement of postlarvae or juveniles. Ideally, sampling should be frequent enough to capture movements related to spawning and recruitment. Direct measurement of patterns of fish movement is also becoming easier with developing techniques such as ultrasonic telemetry (Connolly *et al.*, 2002) and passive integrated transponder (PIT) tags implanted subcutaneously (Parker & Rankin, 2003).

DEMONSTRATING ATTRACTION AND PRODUCTION

Obtaining an accurate picture of fish abundances across several age classes is desirable given the range of possible situations following reef deployment. This diversity is tied to variability in ecology and life history between fish species. Although there are many situations, three hypothetical ones, possible tools of resolution and associated difficulties demonstrating the essential issues in the production and attraction debate are discussed in detail below.

EXCLUSIVE ATTRACTION

Under an 'exclusive attraction' situation, the total number of individuals across reef and control areas remains unchanged throughout a sampling period. All individuals move from control areas onto reefs. Attraction is most likely if all individuals are adults and if juveniles are absent, thus ruling out production

altogether [Fig. 1(a)]. Juveniles may survive for a period on reefs but subsequently perish and do not add to local populations.

EXCLUSIVE PRODUCTION

Under an 'exclusive production' situation, the number of individuals across reef and control areas increases throughout a sampling period and may or may not approach an upper asymptote [Fig. 1(b)]. If the latter occurs, fish abundance is assumed to be a function of the number of reefs deployed. Reaching a 'production' conclusion is a two-stage process. After 1 year, control abundances remain unchanged while reef abundances increase. The first stage is to collect age and length data. Significant numbers of juveniles may represent successful settlement of juveniles onto the reefs that arguably would not have occurred previously in the absence of the reefs. To reach the 'production' conclusion, it must then be demonstrated (in stage two) that the new juveniles remain in the area, grow into a new generation of adults and contribute more individuals to

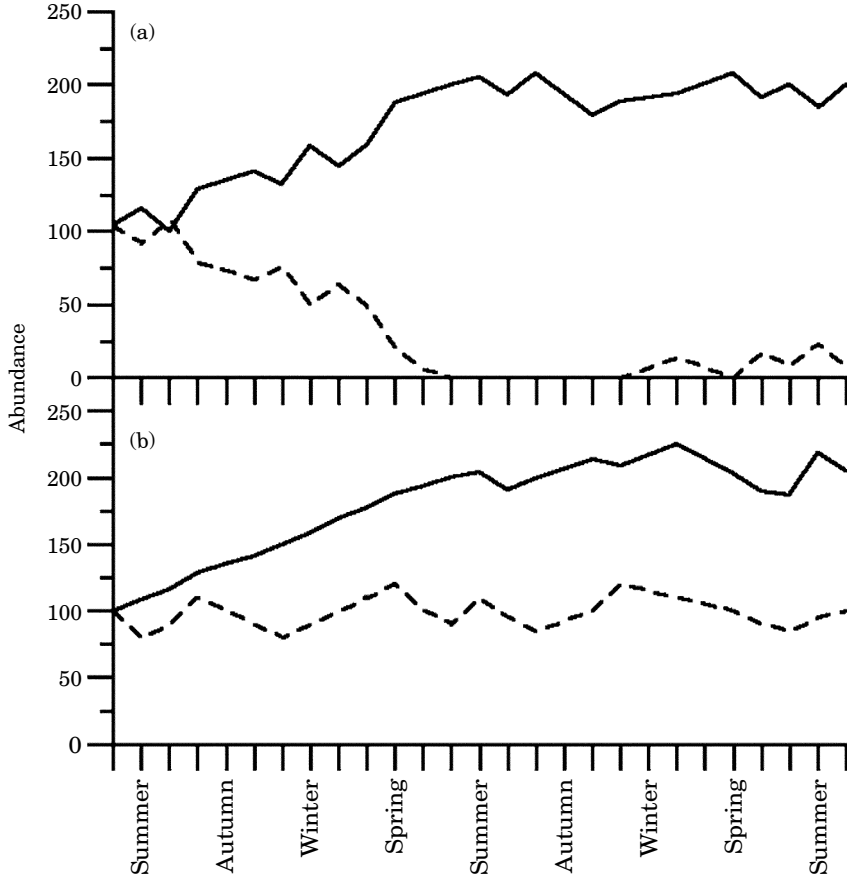

FIG. 1. Possible trends in fish abundance on reefs (—) and controls (– – –) under (a) 'exclusive attraction' and (b) 'exclusive production' control.

the local area themselves in subsequent seasons. Juveniles settling on the reefs eventually contribute to production by migrating off reef units onto control areas once they have reached a certain size as opposed to being forced off prematurely by overcrowding, although this remains a possibility.

SPECIES-SPECIFIC ATTRACTION OR PRODUCTION

Under a more complex 'life history-dependent attraction or production' situation, the life history of a species determines the outcome of a mass recruitment event which may swamp reef and control areas during the first year. If the species involved is a sand and mud obligate, those forced onto reef perish or force themselves onto controls and push their carrying capacity while reef numbers crash [Fig. 2(a)]. If the species involved was a reef obligate, those forced onto control areas would most likely perish or try to occupy reefs, competing for space against those who managed to occupy them first. Abundances on controls would return to a very low level or even zero [Fig. 2(b)]. If the species involved only required reef for one stage of its life history, after initial losses in control areas, those on the reefs may remain there until moving off elsewhere [Fig. 2(c)], possibly to control areas. If the species involved was a generalist, after the swamping event, control numbers would return to normal, reef numbers may settle at slightly higher level, with oscillations as the generalist moves on and off reef [Fig. 2(d)]. In all cases under this category, the sum total of fish abundance in the area will be greater than before reef deployment, but probably at an increase smaller than that expected of the 'exclusive production' situation.

TOOLS TO ISOLATE MECHANISMS

Gut content analysis of fishes on artificial reefs can provide useful information about short-term ingestion of food items (Lindquist *et al.*, 1994), but is unable to distinguish between material that is assimilated from that which is merely ingested. Furthermore, the contribution of primary producers on reefs and elsewhere to the nutrition of carnivorous fishes cannot be ascertained by examining gut contents. Stable isotope analyses has great potential for establishing links between epibenthic producers, lower level consumers and mobile consumers such as fishes, because it determines the degree to which specific isotope signatures are transferred through food webs to fishes (Peterson, 1999). Certain elements such as carbon, that are fundamental to the growth of all organisms, have a rarer, heavier isotope and common, lighter isotope. The ratio of these isotopes typically differs in different types of primary producers. This ratio is (more or less) faithfully transferred through progressively higher levels of a food web. It is a relatively straightforward procedure to obtain samples of fishes, potential prey and primary producers and analyse the isotope ratios on a mass spectrometer. Recent developments in experimental isotopic enrichment mean that isotope analysis can be used even where primary producers lack distinct signatures (Winning *et al.*, 1999).

Isolation of long-term trophic dependence may also be possible by tracing chemicals that leach into the environment from the reefs themselves. Leachates may be absorbed by epibenthos in sufficient quantities to exceed background

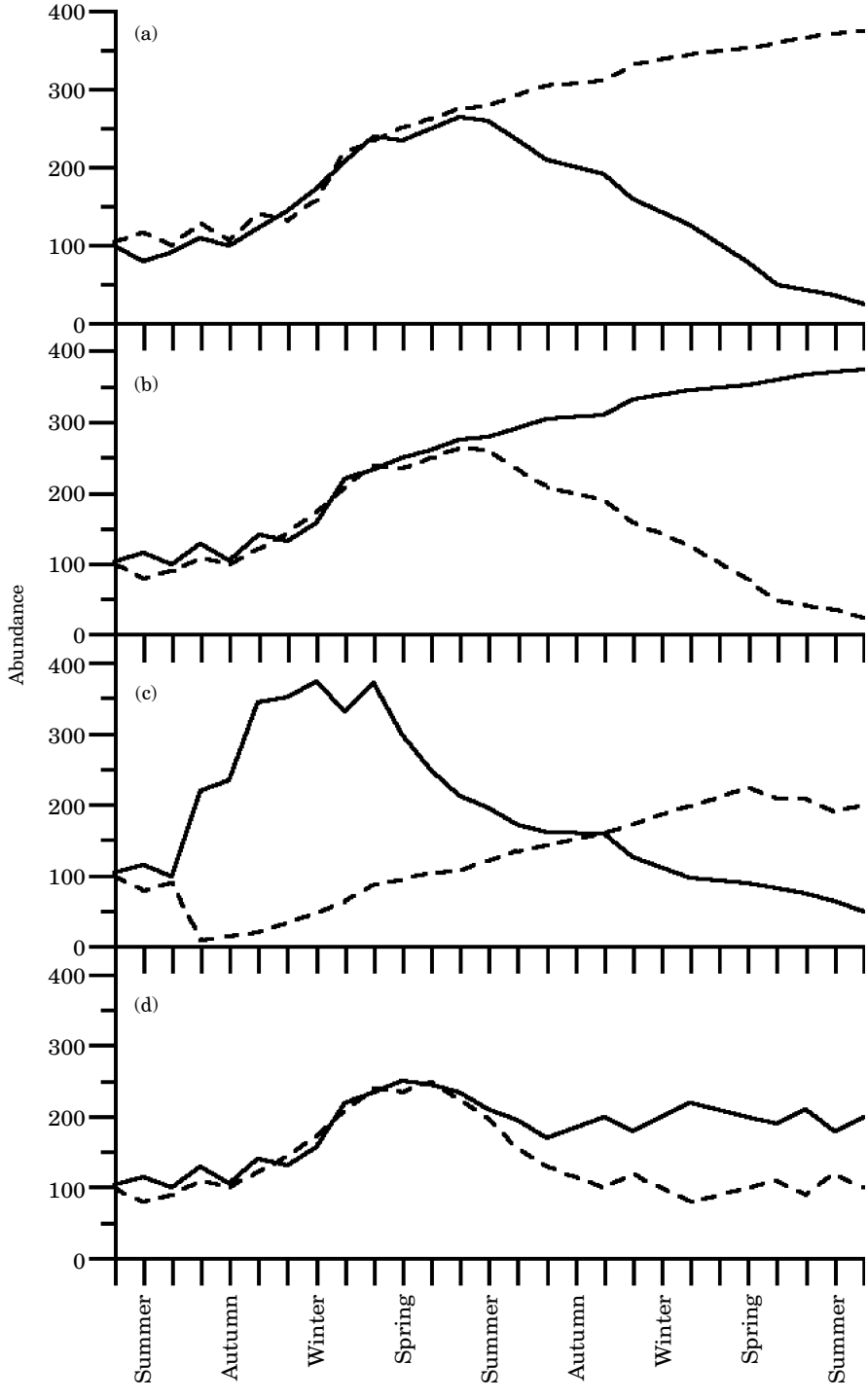

FIG. 2. Possible trends in fish abundance on reefs (—) and controls (– – –) under life-history dependent 'attraction or production' situation for (a) a sand and mud obligate species, (b) a reef obligate species, (c) a 'temporary' reef obligate species and (d) a generalist species.

concentrations and serve as potential markers of dependency upon reef epibenthic biomass by recruits. For example, potential leachates from reefs constructed from polyvinyl chloride (PVC) pipes include phthalates, organotin compounds and heavy metals (*e.g.* lead) occurring in plasticizers and stabilizers used during the PVC manufacturing process (Mersiowsky *et al.*, 2001). Although the use of reef leachates as a tracer is yet to be attempted, the detection of such compounds in animal tissues is becoming relatively straightforward through advances in mass spectrometry.

ADDITIONAL DIFFICULTIES

Ideally, artificial reef experiments should feature sufficiently rigorous designs to distinguish the effects of attraction and production. Central to this is the ability of designs to detect predicted changes in fish abundance using methods that can sufficiently measure the attractive component of artificial reefs. Sampling regimes should be tailored to species of interest, capturing any peaks and troughs and noticeable movements that may occur between controls (or elsewhere) and reefs. For example, if any observed change in abundance of fishes is to be attributed to fishes moving onto reefs from elsewhere, sampling should detect a decrease in the abundance of fishes in the region surrounding reefs that is equal to the increase in abundance at the reefs. Where attraction occurs, the net abundance of fishes at reefs and surrounding areas should not change. Hypotheses should be tested that predict the extent of influence of the reefs and when assessing the productive potential of reefs where attraction may be occurring, it is necessary to define the region that is subject to the 'attractive' properties of the reef. Any increase in fish abundance observed in the region *plus* the reef would be production because the region would encompass all exchanges of individuals to and from the artificial reef. Establishing dietary linkages between resident cohorts and reef and control sites would strengthen evidence in favour of either outcome. Unfortunately, while huge resources have been spent on the construction and deployment of artificial reefs for enhancement of commercial and recreational fisheries (particularly in South East Asia), rigorous experimental studies that distinguish between the effects of attraction and production have not been published (note that Polovina & Sakai's (1989) study was not strictly experimental).

One promising avenue for artificial habitat research is to develop the logic and experimental design of experiments on less mobile animals in simpler systems (*e.g.* gastropods on a rocky shore, Webley, 2002). Lessons learned from such studies will be more difficult to apply given the mobility of fishes, but recent advances in telemetry and tagging techniques are making the tracking of fish movements easier.

Difficulties presented by the movement of fishes may be partly addressed by development of age and length distributions and length and mass distributions, together with the use of dietary resolution techniques such as gut content and stable isotope analyses. Use of such distributions and techniques should further improve the capacity of experimental designs to attribute changes in fish abundance to attraction or production, primarily through inclusion or exclusion of diet as a factor driving movement of individuals on and off artificial reefs.

Studies that have included explicit comparisons between artificial reefs and associated soft bottom controls have so far been unable to distinguish between attraction and production when explaining increases in the abundance of fishes at reefs. Lack of rigorous experimental designs incorporating the collection of longitudinal data to highlight long-term trends in fish abundance continues to be a problem in the field of artificial reef research. As well as re-emphasising gaps reported previously (Bohnsack & Sutherland, 1985; Pickering & Whitmarsh, 1997), this paper highlights the role adequate sampling regimes can play in isolating trends in fish abundance. Resolution of such trends (often related to key life history events) can contribute to the isolation of attraction or production as mechanisms driving changes in population size and demography, both of which are major determining factors in the management and exploitation of commercial and recreational fish stocks. Establishing dietary links between fish cohorts and epibenthic food sources that become available on artificial reefs should also make isolation of these mechanisms easier by inclusion or exclusion of diet as a factor driving the settlement and/or departure of individuals at and from artificial reefs at varying stages of life history. Establishing such links and resolving growth and movement regimes has become easier with the development of new tools such as otolith microchemistry, telemetry, tagging and stable isotope analyses.

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