

Why do fishers fish where they fish? Using the ideal free distribution to understand the behaviour of artisanal reef fishers

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Abstract: We used the theory of the ideal free distribution (IFD) as a framework to understand the mechanisms underlying fishing site selection by Anguillian artisanal fishers exploiting shallow-water coral reefs. Contrary to the predictions of IFD, fishers did not distribute themselves so that average reward was equal among fishers using different fishing methods or among fishers using the same method. In addition, fishing pressure did not increase with resource availability. Key assumptions of the IFD were not met. The distribution of Anguillian fishers was not “ideal” because lack of knowledge prevented fishers from choosing fishing grounds with the greatest rewards. Not all fishers sought to maximise profit. In addition, all fishers were not “free” to distribute themselves among reefs owing to variation in social, economic, and physical characteristics of fishers that constrained fisher movements and ability to extract resources. This study shows that as a null model the IFD is useful to frame studies designed to gain detailed insights into the complexity and dynamics of a small-scale fishery. Alongside ecological data, this framework may inform efficient and effective development of reef and fishery management practice.

Résumé : Nous utilisons la théorie de la distribution libre idéale (« IFD ») comme cadre pour comprendre les mécanismes sous-jacents de la sélection des sites de pêche par les pêcheurs artisanaux d'Anguilla qui exploitent les récifs coralliens de faible profondeur. Contrairement aux prédictions de l'IFD, les pêcheurs ne se répartissent pas de façon à ce que le rendement de la pêche soit égal pour tous les pêcheurs qui utilisent les différentes méthodes de pêche, ni pour les pêcheurs qui utilisent la même méthode. De plus, la pression de la pêche n'augmente pas en fonction de la disponibilité des ressources. Des présuppositions importantes de l'IFD ne se réalisent pas. La répartition des pêcheurs d'Anguilla n'est pas « idéale » parce que l'absence de connaissances empêche les pêcheurs de choisir les sites de pêche avec les meilleurs rendements. De plus, tous les pêcheurs ne cherchent pas à maximiser leur profit. Enfin, tous les pêcheurs ne sont pas « libres » de se répartir sur les récifs parce que la variation de leurs caractéristiques sociales, économiques et physiques entravent leurs déplacements et leur capacité à extraire les ressources. Notre étude démontre que la IFD peut utilement servir de modèle nul pour élaborer des études visant à obtenir des perspectives détaillées sur la complexité et la dynamique d'une pêche commerciale à petite échelle. Avec des données écologiques, ce cadre d'étude peut permettre un développement efficace et effectif des pratiques de gestion des récifs et des pêches commerciales.

[Traduit par la Rédaction]

Introduction

Small-scale artisanal fisheries are widely recognised as having a significant impact on the health of coral reefs (Hughes 1994; Hawkins and Roberts 2004; Wilkinson 2004). Fishing on coral reefs reduces the abundance and biomass of exploited species, many of which perform important ecological functions (Pauly et al. 2002; Hughes et al. 2003; Bellwood et al. 2004). The exploitation of predatory fishes can have a cascading effect on coral ecosystems, resulting in outbreaks of coral-eating starfish and grazing urchins, which

lead to coral loss and macroalgal overgrowth (McClanahan 1994; Dulvy et al. 2004; Hughes et al. 2007). As three-quarters of the world's coral reefs lie within developing countries in which subsistence economies predominate, the impact of coral reef fisheries is not only of ecological but also of great social and economic concern (Salvat 1992; Whittingham et al. 2003).

Although the importance of considering fisher behaviour for successful fisheries management has been emphasised (Hilborn and Walters 1992; Charles 1995; Wilen et al. 2002), our understanding of fisher behaviour, particularly for

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small-scale fisheries, is at best rudimentary. Small-scale fishers tend to be heterogeneous in their rates of stock depletion and fishing behaviour, thus their response to management initiatives can also be diverse (Pet-Soede et al. 2001; Salas and Gaertner 2004; Gelcich et al. 2005). Because behavioural decisions effectively underpin where fishers elect to fish, there is great interest in the discovery of rules explaining the distribution of small-scale fishers that could help to design management that promotes sustainable harvests.

The theory of the ideal free distribution (IFD), which predicts the spatial distribution of consumers in relation to the distribution of resources (Fretwell and Lucas 1970), may provide a suitable framework for understanding the harvesting behaviour of fishers. The IFD makes two key assumptions. In relation to fishers, the IFD assumes that fishers have "ideal" knowledge of the distribution of their target species and are "free" to move between fishing grounds without constraint of movement or ability to extract resources (Kacelnik et al. 1992). As a result, the theory makes two predictions. Firstly, fishers will distribute themselves so that the average reward, or catch, should be equal for all fishers, and secondly, fishing pressure should increase with resource availability (Sutherland 1996). Fretwell (1972) himself recognised that the assumptions are unlikely to be met. However, IFD theory has proved influential as a null model from which the deviations can identify important factors that determine the distribution of foragers (Sutherland and Parker 1985; Kacelnik et al. 1992).

The IFD framework has previously been used to understand the spatial dynamics of fleets in large-scale temperate fisheries (Abrahams and Healey 1990; Gillis et al. 1993; Swain and Wade 2003). As is the case in studies of animal behaviour, the results of tests of the various predictions and assumptions of the IFD have been mixed. In no case have fleets, and therefore implicitly fishers, perfectly followed an IFD. Deviations have been due to variation in competitive ability of fishers or their boats, tradition and inertia to change, attitudes toward personal and financial risk, and lack of perfect knowledge of the resource (Holland and Sutinen 1999; Rijnsdorp et al. 2000; Swain and Wade 2003). Because fishers target prey that can not be seen, their "foraging" decisions are based on knowledge of prey distribution derived from their catches, observations of their potential competitors' distributions, and perception of other constraints and hazards. Furthermore, given that people differ in their behaviour and the utility they seek to maximise (Dawnay and Shah 2005), it is not surprising that that fishers do not follow a perfect IFD. By identifying the factors causing departures from the IFD model, we can improve our understanding of the optimisation criteria used by fishers, as well as the drivers and constraints that influence fishers' decisions regarding where, when, and how to fish.

The IFD has never been applied to small-scale tropical fisheries. Artisanal fisheries are often very heterogeneous in terms of fisher composition, target species, and gear type and efficiency. Fishers involved in these fisheries may be less likely to have uniform patterns of behaviour than those in large-scale profit-oriented commercial fisheries (Salas and Gaertner 2004). It can be difficult to understand the complexities of reef resource use and fisher behaviour, thus the

IFD may provide a suitable framework to structure a study into the behaviour of artisanal fishers and its impacts on spatial distribution of fishing effort.

The purpose of this study was to test the applicability of the IFD concept to understand the spatial distribution of coral reef fishers on the Caribbean island of Anguilla. We first investigated whether Anguillian fishers exhibit an ideal free distribution by testing the predictions that fisher reward is equal across fishers and that fishing pressure is directly proportional to the abundance of target species. We then tested two key assumptions of IFD, namely that fishers had ideal knowledge of stock abundance on their fishing grounds and freedom from constraint of movement and ability. The identification of the causes of violations to the IFD assumptions allowed us to build a detailed picture of what drives the spatial patterns in this artisanal fishery. Our results have implications for the effective implementation and selection of fisheries management practices.

Materials and methods

Study site

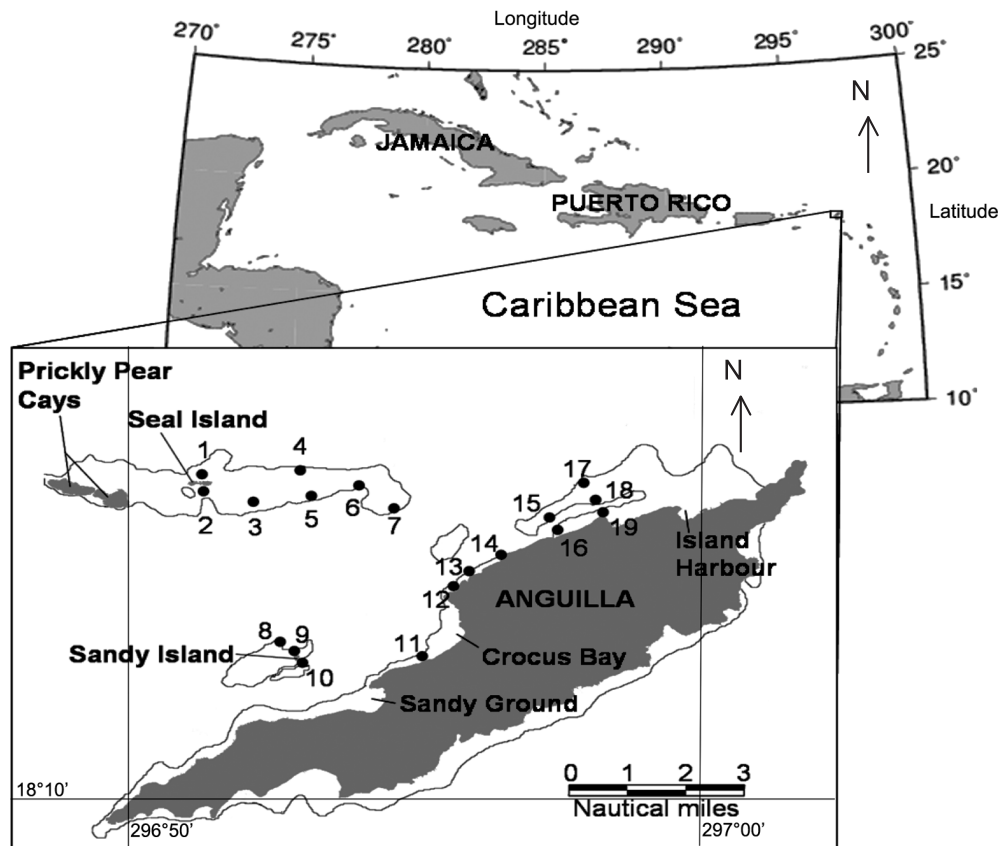
The study was undertaken on Anguilla, British West Indies (Fig. 1), where the fishing industry is largely artisanal. There are approximately 130 outboard-powered open-top fishing vessels (Hoggarth 2001), most of which are between 5 and 10 m in length. This study focused on a proportion of the fleet, the small inshore coral reef fishery, that targets reef fish (groupers (Serranidae), parrotfish (Scaridae), and surgeonfish (Acanthuridae)) and spotted spiny lobster (*Panulirus guttatus*), known locally as crayfish. The expanding luxury tourism industry has created a high and growing demand for crayfish (Wynne and Côté 2007). There is also a high demand for reef fish, which are primarily consumed by local people. Anguilla currently has only two technical restrictions: a ban on taking berried female crayfish and a minimum trap mesh size. There are no no-take areas and no catch or effort restrictions (Government of Anguilla 2000).

Study subjects

Interviews were conducted with 42 fishers from three harbours on the north side of the island (Fig. 1) during April and May 2005. Fishers were categorised into four types: trap fishers who target reef fish, trap fishers who target crayfish, fishers who hand-capture crayfish by snorkelling and free diving on the reefs at night, and spear fishers who target reef fish. If fishers engaged in more than one type of fishing, they were categorised by their main fishing type. All fishers in Anguilla who relied on fishing the coral reefs for all or part of their income were interviewed ($n = 25$). In addition, we interviewed as many fishers who fished for personal consumption as possible ($n = 17$). These fishers were either fish trap or spear fishers.

Interviews with fishers consisted of a series of highly structured, closed questions to provide quantitative data and open-ended questions to generate complementary qualitative data. Interviews were tape-recorded and transcribed verbatim. Transcripts were systematically coded according to each variable of interest to ensure that data were not used selectively.

Fig. 1. The distribution of study sites (●) around Anguilla and nearby cays. The thin outline (—) represents the shallow (<10 m) reef areas. 1 nautical mile = 1852 m.



Triangulation was employed to increase confidence in the accuracy of data collected through fisher interviews. Triangulation is a method of establishing the accuracy of information by comparing three or more types of independent points of view on data sources (Bruce et al. 2000). Data for triangulation were obtained by repeated interviews with key informants, by accompanying fishers on fishing trips, and by daily observations of fishers over 7 weeks.

IFD prediction 1: fisher reward

To test the first IFD prediction, that all fishers have equal rewards, catch weights were collected for between five and 18 fishing trips for each fisher. Catches were either weighed directly (to the nearest 0.1 kg, with hand scales) or weights were extracted from fish market logbooks and fishers' personal records. Species of different value were weighed separately. Fisher reward was calculated as gross profit per unit effort (PPUE) per trip and was calculated in US\$ as

$$(1) \quad \text{PPUE} = \frac{(V - C)}{T}$$

where V is the catch value, calculated using the tourist consumption or fish market price per unit weight (kg), depending on the species; C is the total cost of the trip, including fuel, gear, and wages, where applicable; and T is the total time (h), including time spent fishing, collecting bait, and preparing gear. The use of time spent fishing allowed all fishing methods to be compared. We did not explicitly consider the number of traps set or hauled; however, there was a

highly significant relationship between time spent fishing and number of traps (fish traps, $R^2 = 0.75$, $F_{[1,162]} = 490.69$, $P < 0.001$; crayfish traps, $R^2 = 0.86$, $F_{[1,58]} = 353.74$, $P < 0.001$).

The equality of PPUE across fishers was examined using a two-level nested analysis of variance (ANOVA), with PPUE as the dependent variable. Fishing method was included as a fixed factor, and fisher, a random factor, was nested within fisher type. Individual PPUE values were plotted with 95% confidence intervals to highlight differences.

IFD prediction 2: fishing pressure and resource distribution

To test the second IFD prediction, that fishing pressure is positively related to resource abundance, fish abundance was estimated at 19 sites between April and June 2004 (Fig. 1). Site selection was based largely on accessibility. All sites were fished to some extent. Five haphazardly located belt transects (6 m × 30 m) were surveyed at each site at depths of 5 m and 10 m. Surveys at sites 3, 11, and 15 (Fig. 1) could only be conducted at 5 m. The abundance of all fish species was recorded while swimming at 3 m·min⁻¹. In the analyses, we considered only species of the three main fish families targeted by fishers (Serranidae, Scaridae, Acanthuridae). The average abundances for each species were summed for each site.

In April and May 2005, the number of traps within a 50 m radius of each of the 19 sites was recorded once per week for 6 weeks. Fishing pressure at each site was obtained by

averaging these weekly counts. To test whether fishers exhibit an ideal free distribution, the relationship between proportional fishing pressure and fish abundance at each site was analysed using a Spearman rank correlation. Because a non-significant correlation was obtained (see Results), indicating that fishers do not distribute themselves in an ideal-free manner, we performed further analyses to determine whether the assumptions of the IFD theory were violated and why.

IFD assumption 1: freedom of movement and fisher ability

Constraints on movement and ability affecting fisher PPUE were identified during interviews. These constraints were investigated on two levels: (i) constraints that affected fishers' choice of fishing method, their ability to switch fishing method, and the impact on PPUE, and (ii) constraints that affected PPUE within a fishing method. For the latter, we focused on spear fishers and fish trap fishers, owing to limited sample sizes for other types of fishers.

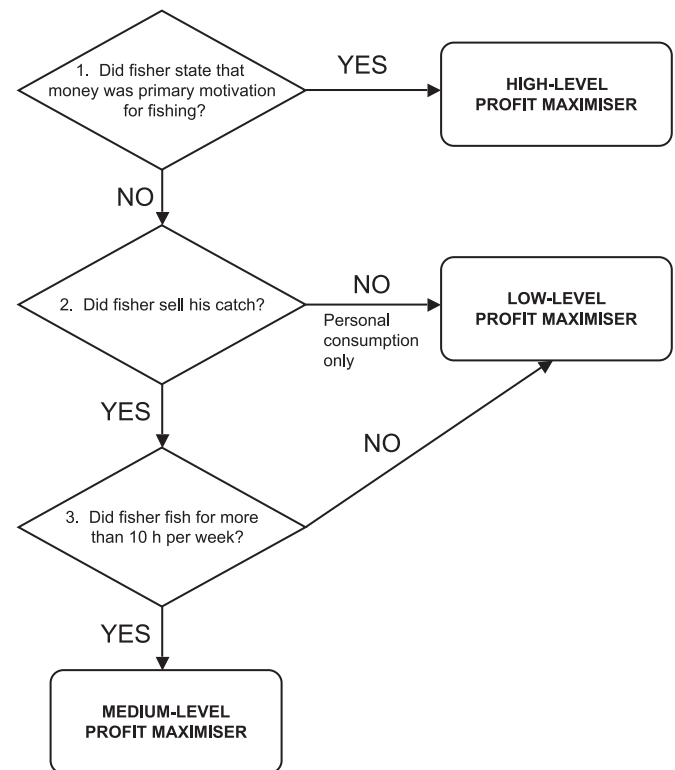
We identified three factors that prevent fishers from switching fishing method: fisher age, profit-maximising behaviour, and fisher ability (i.e., "skill and capability", sensu Sen 1985). The latter is assumed under IFD to be equal among foragers (Parker and Sutherland 1986; Gillis 2003). Profit-maximising behaviour is important within the context of the IFD theory because IFD assumes that fishers pursue the goal of achieving the highest rewards possible. Fishers were therefore categorised into three levels of profit maximisation (low, medium, and high), using the decision process illustrated in Fig. 2. This categorisation is based on three variables that are known to determine the behaviour of Anguillian fishers (Abernethy 2005): motivation to fish (money or other), use of catch (personal consumption or sale), and the amount of time spent fishing (less than or more than 10 h per week). Differences in PPUE of fishers of different profit-maximising levels were analysed using a one-way ANOVA.

Variation in the ability of fishers, or "skipper effect" (Acheson 1981; Palsson and Durrenberger 1983), was examined in the Island Harbour community ($n = 32$ fishers). As self-assessment of ability is likely to be biased, we instead asked each fisher to identify the three "best" fishers from a list of Island Harbour fishers (based on their observations and other information regarding individuals fishing takes and efficiency). All four fishing methods were represented. The number of votes scored for each fisher gave a more objective measure of fisher ability than self-assessment. The number of votes was compared among fishing methods and related to actual PPUE of fishers.

In addition, qualitative factors that prevent fishers from switching fishing method were also noted. We paid particular attention to the fishers' perception of risk, i.e., the likelihood of physical harm to self or gear, because the IFD assumes that all fishers have the same risk propensity.

The constraints generating variation in PPUE within fishing method, focussing specifically on fish trap fishers and spear fishers, were identified in interviews as time spent fishing per week, age of fisher, lifetime experience (current number of hours fished per week multiplied by the number of years spent fishing), importance of fishing to fishers' livelihoods (percentage of fishers' income derived from fishing),

Fig. 2. Flowchart illustrating the process used to determine the level of profit maximisation behaviour of an individual fisher given three key variables that are known to determine the behaviour of Anguillian fishers.



and monetary cost (Abernethy 2005). For the latter, distance travelled to and from fishing sites was used as a proxy for the cost of fuel per trip. The effect of each of these variables on PPUE was examined. For the analyses of fish trap fishers, PPUE was transformed to a log scale. Although Anguilla has no tradition of ownership of fishing grounds, other qualitative constraints on movement were investigated by asking fishers why they did not fish at certain sites.

IFD assumption 2: ideal knowledge of fishing grounds

To examine the assumption of ideal knowledge, fishers were asked to rank each of the 19 sites in terms of the abundance of target fish species from 1 (lowest abundance) to 5 (highest abundance). To ensure comparability among fishers' scores, fishers were asked to rank the best site(s) as 5, then use that score as a basis for ranking the other sites. If a site was not known, the particular site was not included for the particular fisher in the analyses. A Spearman's rank correlation was used to test the relationship between relative fish abundance (derived from the underwater surveys) and the mean ranked abundance perceived by fishers. This analysis was repeated for each fishing method separately.

In addition, fishers' ability to accurately predict abundance was regressed against the navigable distance of sites from harbour. Navigable distances were measured, using the GIS software ArcView GIS 3.2 (ESRI, Redlands, California), as the shortest distance between a harbour and each site while avoiding shallow water and land. Fisher knowledge accuracy for each site was calculated by first transforming

actual fish abundance at each site to fit a five-point ranked scale, with the site of highest abundance given a score of 5 and then a ranked relative abundance (RRA) was calculated for each site as

$$(2) \quad RRA_i = 5 \left(\frac{A_i}{A_h} \right)$$

where A_i was the actual abundance at site i , and A_h was the actual abundance at the site with highest abundance. Then the absolute difference between the ranked relative fish abundance and the mean ranked abundance perceived by fishers was calculated. These differences were then subtracted from 5 so that low accuracy had a low numerical value and high accuracy had a high numerical value.

Results

IFD prediction 1: fisher reward

There were significant differences in mean PPUE among fishing methods (two-level nested ANOVA: $F_{[3,38.42]} = 198.58$, $P < 0.001$). Fishers who capture crayfish by hand had a significantly higher PPUE than fishers using other methods (mean \pm standard error (SE): fish traps, 21.32 ± 11.45 , $n = 16$; crayfish traps, 24.85 ± 9.54 , $n = 6$; spear fishers, 34.98 ± 12.45 , $n = 16$; crayfish hand-capture, 230.26 ± 36.64 , $n = 4$). Differences among methods remained when crayfish hand-catchers were excluded from the analysis ($F_{[2,35.2]} = 4.16$, $P = 0.02$), with spear fishers having a significantly higher PPUE than trap fishers. There was no difference in PPUE between fish and crayfish trap fishers ($F_{[1,20.17]} = 0.42$, $P = 0.52$). Individual fishers also differed in PPUE within fishing method ($F_{[38,372]} = 7.06$, $P < 0.001$; Fig. 3).

IFD prediction 2: fishing pressure and resource distribution

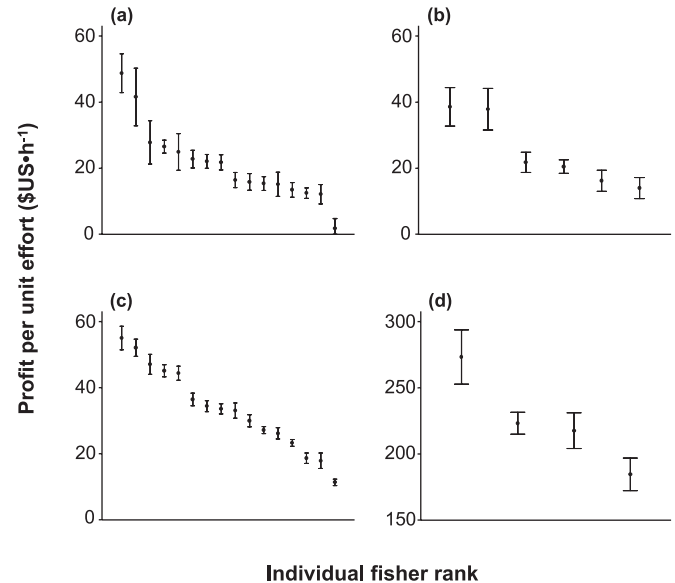
The average number of traps at each site varied from 0 to 14. There was greater variation between sites in trap numbers than between repeated counts within sites (ANOVA: $F_{[18,95]} = 10.53$, $P < 0.001$). There was no relationship between fish abundance at a site and the mean number of traps at each site ($R_s = -0.01$, $n = 19$, $P = 0.96$).

IFD assumption 1: freedom of movement and fisher ability

Choice of method and ability to switch method

Interviews revealed three qualitative factors that prevent fishers from switching to hand-capturing crayfish, the most profitable fishing method: risk to fisher, the lack of a fishing companion, and the value of leisure time. Some fishers considered it too dangerous to snorkel on the reef at night, whereas others were prepared to take this risk, but not without a fishing partner (and were unable to find one). Other fishers considered night fishing a time-consuming activity that impacted on their leisure time. In addition, fish trap fishers felt that they did not have the necessary free-diving skill to catch crayfish by hand, whereas spear fishers and crayfish trap fishers did.

Fig. 3. Profit per unit effort (PPUE, $\text{\$US}\cdot\text{h}^{-1}$) of individual (a) fish trap fishers, (b) crayfish trap fishers, (c) spear fishers, and (d) crayfish hand-catchers, exploiting coral reef resources in Anguilla. Means are shown ± 1 standard error (SE). Sample sizes varied from $n = 4$ to $n = 16$. Fishers are ranked in order of decreasing PPUE.



There was no significant overall difference in the age of fishers using different methods ($F_{[3,38]} = 1.81$, $P = 0.16$), although fish trap fishers tended to be older than fishers using other fishing methods (fish traps, 49 ± 3 years; crayfish traps, 41 ± 6 years; spear fishers, 39 ± 2 years; crayfish hand-capture, 43 ± 5 years). In addition, there was no relationship between the age of a fisher and PPUE ($R^2 = 0.08$, $F_{[1,40]} = 0.34$, $P = 0.58$).

All crayfish hand-catchers were high-level profit maximisers, whereas fewer of the other three fisher types fell into this category (fish traps, 12%; crayfish traps, 16%; spear fishers, 12%). The majority of fish trap (69%) and crayfish trap (84%) fishers were medium-level profit maximisers. Most spear fishers (88%) and some fish trap fishers (19%) were low-level profit maximisers.

As expected, there was a significant difference in PPUE between profit maximiser levels when all fishers were considered ($F_{[2,39]} = 9.8$, $P < 0.001$). High-level profit maximisers had significantly higher PPUE than both medium- and low-level profit maximisers (both Tukey tests > 87.11 , $P = 0.001$). However, when crayfish hand-catchers were excluded from the analysis, there was no significant difference in PPUE between profit maximiser levels ($F_{[2,35]} = 0.45$, $P = 0.64$).

Perceived ability of fishers varied among fishing methods ($F_{[3,28]} = 9.58$, $P < 0.001$). Crayfish hand-catchers received significantly more votes than fishers in the other groups (crayfish hand-capture vs. all other methods: all Tukey > 8 , $P < 0.002$). PPUE increased with perceived ability ($R_p = 0.77$, $n = 32$, $P < 0.001$; Fig. 4).

Within fishing method

Fish trap fishers were constrained in their trap placement for a number of reasons. Thirty-eight percent of fishers stated

that they avoided other individuals and often travelled further to do so, indicating that fishers traded off maximising profit to avoid potential conflict. The same proportion (38%) did not move from their general fishing areas because they felt that fish abundance was sufficient to meet their needs. Both these observations indicate that fishers use criteria other than profit maximisation: conflict avoidance in the first case and consumption satisfaction in the second. Nearly half (44%) of fishers believed that the area around Sandy Island (sites 8, 9, and 10) was a no-take marine protected area (MPA) and did not fish there. This may be because it is a proposed MPA site and because it is a tourist snorkelling and diving area. In addition, 25% of fishers mentioned time constraints, and 19% said that cost of fuel and gear prevented them fishing further from harbour.

For fish trap fishers, age of fisher was the main determinant of PPUE, with older fishers having greater PPUE ($R^2 = 0.27$, $F_{[1,13]} = 4.85$, $P = 0.046$; Fig. 5a). There was no relationship between fisher age and the number of traps owned ($R_p = -0.43$, $n = 15$, $P = 0.10$). There was no significant relationship between PPUE and distance travelled per trip, amount of time spent fishing per week (Fig. 5b), fisher lifetime experience (Fig. 5c), and percentage of income derived from fishing (all $R^2 < 0.04$, all $F_{[1,13]} < 0.42$, all $P > 0.52$). Amount of time spent fishing per week was not correlated with age ($R_p = -0.15$, $n = 14$, $P = 0.60$) but was positively correlated with experience ($R_p = 0.91$, $n = 14$, $P < 0.001$). Age and experience were not correlated ($R_p = 0.14$, $n = 14$, $P = 0.60$).

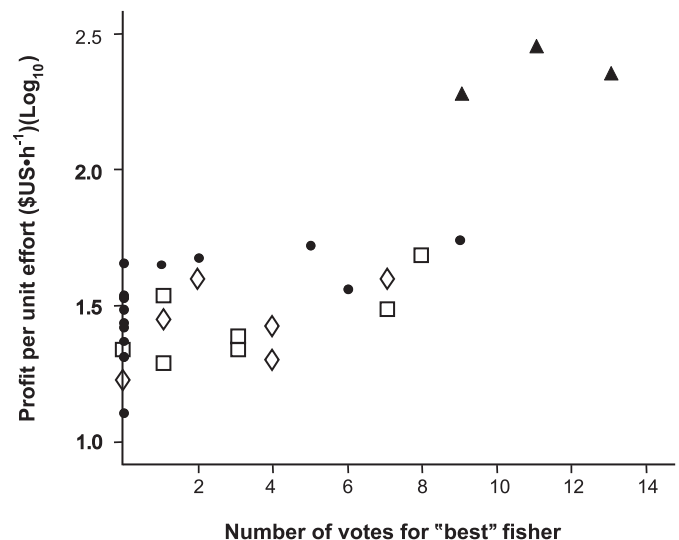
Spear fishers were constrained in their ability to move between sites for two reasons. Again, a high proportion (42%) of fishers believed that Sandy Island was an MPA and therefore avoided this area. Spear fishers preferred not to travel very far, with most fishers (84%) choosing sites close to their home. Competition was not a strong factor constraining spear fishers choice of site, with few fishers (12%) intentionally avoiding areas where there were other individuals.

Younger spear fishers had a greater PPUE than older spear fishers ($R^2 = 0.30$, $F_{[1,13]} = 5.70$, $P = 0.03$; Fig. 5d). Fishers who spent more time fishing per week also had greater PPUE ($R^2 = 0.70$, $F_{[1,13]} = 30.25$, $P < 0.001$; Fig. 5e), as did spear fishers with more lifetime experience ($R^2 = 0.32$, $F_{[1,13]} = 6.22$, $P = 0.03$; Fig. 5f). The amount of time spent spear fishing per week correlated negatively with age ($R_p = -0.60$, $n = 15$, $P = 0.02$) but positively with experience ($R_p = 0.73$, $n = 15$, $P = 0.002$). Age and experience were not correlated ($R_p = -0.03$, $n = 15$, $P = 0.92$). The amount of income was not investigated because spear fishers primarily fished for personal consumption only.

IFD assumption 2: ideal knowledge of fishing grounds

There was no relationship between our measure of fish abundance and the abundance perceived by fishers at each site ($R_s = -0.33$, $n = 19$, $P = 0.17$). This result held when each fishing method was considered separately (all $R_s = -0.44$ to -0.30 , all $n = 19$, all $P > 0.06$). Crayfish trap fishers were included because they went to sites to catch fish for bait. Crayfish hand-capture fishers were also included because all did additional fishing for reef fish. This result also held when fishers who did not fish

Fig. 4. The relationship between mean profit per unit effort (PPUE, \$US·h⁻¹) and the number of “best” fisher votes obtained by 32 fishers from the Anguillian port of Island Harbour. ◇, crayfish trap fishers; ▲, crayfish hand-catchers; ●, spear fishers; □, fish trap fishers.



the entire reef, and therefore might not have experience at all sites, were excluded ($R_s = -0.34$, $n = 19$, $P = 0.16$).

The accuracy of fishers' assessment of fish abundance decreased as the navigable distance from port increased ($R^2 = 0.28$, $F_{[1,17]} = 6.46$, $P = 0.02$; accuracy = $-0.20(\text{distance}) + 4.53$).

Discussion

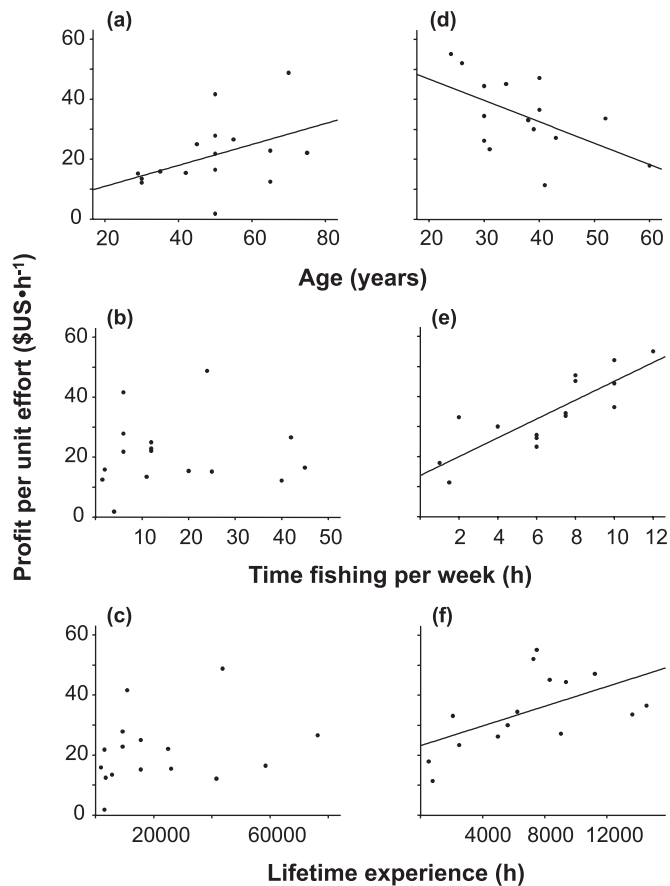
The coral reef fishers of Anguilla do not exploit coral reefs following an ideal free distribution. The two predictions of the ideal free distribution were not met: fishers did not distribute themselves in relation to resource abundance and there was marked interindividual variation in profit per unit effort. We found that in violation of the assumptions of IFD, fishers were not free from constraints of movement or ability. Variation in the social, economic, and physical characteristics of fishers prevented them from changing fishing method and allowed some fishers to perform better than others when using the same method. In addition, a lack of knowledge of reef resources prevented fishers from choosing fishing grounds with the greatest rewards.

To successfully implement management initiatives within a fishery, a clear understanding of the dynamics of resource use is required, particularly to predict fisher responses to management. In the case of the Anguillian fishery, this understanding was gained through testing the assumptions of the theory of ideal free distribution — the freedom of movement and fisher ability and ideal knowledge — and observing the causes of any deviations. Freedom of constraint was investigated on two levels: the constraints on fishers' ability to choose or switch fishing method, and constraints within fishing method (for fish trap and spear fishers).

Freedom of movement and fisher ability

PPUE between fishing methods was largely driven by economics and, to a lesser extent, by ability and risk-taking

Fig. 5. The relationships between profit per unit effort (PPUE, $\text{\$US}\cdot\text{h}^{-1}$) and age (years), time spent fishing per week (h), and lifetime experience (h) for fish trap fishers (a, b, c, respectively) and spear fishers (d, e, f, respectively). The regression equations for significant relationships are (a) $\text{PPUE} = 0.006(\text{age}) + 0.99$; (b) $\text{PPUE} = -0.71(\text{age}) + 61.05$; (d) $\text{PPUE} = 3.14(\text{time spent fishing per week}) + 13.7$; and (f) $\text{PPUE} = 0.002(\text{lifetime experience}) + 23.14$.



behaviours. Those fishers that hand-captured crayfish were substantially more successful than all those using other methods, raising the question of why all fishers do not fish this way, particularly those who used traps to catch the same species. Crayfish hand-catchers were identified as profit-maximising individuals, whereas crayfish trap fishers, who were also full-time fishers and completely dependent on fishing for income, were generally not profit maximisers. The latter ($n = 5$) valued their evening leisure time much more than the extra money that could be earned by diving at night for crayfish. For crayfish trap fishers, fishing was not only a source of income or food, it represented an autonomous and enjoyable way of life.

The assumption that all individuals seek to maximise profits underpins the theory of the IFD, and often this rational fisher response to regulatory frameworks is assumed by policy makers. However, the notion that fishers respond solely to monetary profit stimuli in making decisions is contentious. Alongside this Anguillian case study, other studies have shown that for both small-scale and commercial fishers, profit maximisation criteria are modified by social interactions, so that fishers trade off profit with other values, e.g.,

safety, comfort, and making time available (Béné and Tewfik 2001; Cabrera and Defeo 2001; Salas and Gaertner 2004). As a result, the expected response of fishers to management may be affected by these interactions. A better understanding of fisher decision making means that management decisions that are ineffective or even result in disastrous ecological consequences (Dinmore et al. 2003) could be avoided.

The perceived ability (skipper effect) of fishers was also identified as a significant factor influencing PPUE, with crayfish hand-catchers identified by their community as the best fishers. Although it has been argued that variance in catch can be largely explained by differences in technology and effort, and not by the intrinsic ability of the fisher himself (Palsson and Durrenberger 1990), there was no evidence of this in the Anguillian fishery. In favour of the skipper effect idea, interviews indicated that crayfish hand-catchers observed and understood well the dynamic nature of their fishing grounds, such as the seasonality of the species and the effects of tides and currents, as well as suitable habitat. Crayfish hand-catchers adjusted their fishing practice accordingly in order to maximise their profit.

On a finer scale, variation in PPUE and constraints on freedom within two fishing methods (fish trap fishing and spear fishing) were examined. Within the fish trap fishers, older fishers had higher PPUE than younger fishers. There are many reasons why this may be so. Older fishers may have a better understanding of reef dynamics and thus could respond faster to shifting fish abundance. This variation in ability to detect or predict changes in fish abundance could result in those fishers with high detection ability setting their traps at sites of high abundance first, leaving less able fishers to fish in less suitable areas. Older fishers may also be more patient and have better judgement of how and where to place traps on a microscale. However, lack of understanding of reef dynamics does not explain variation in PPUE between spear fishers. For most spear fishers, fishing was primarily a recreational activity for consumptive purposes, undertaken at convenient sites, close to home. Constraints that contributed to variation in spear fisher PPUE were age and time spent fishing per week. Spear fishing is a young man's activity, with physical fitness and practice improving PPUE.

It is clear that the differences in fishers' competitive ability are an important determinant of the pattern of resource use by fishers in Anguilla. This is not an unexpected result. Investigations into the application of IFD in both ecological systems and fisheries have shown the importance of considering between-forager differences in abilities to increase the realistic application of IFD models (Parker and Sutherland 1986; Abrahams and Healey 1990; Holland and Sutinen 1999). Understanding how and why fishers differ in their competitive ability can also have a significant effect on the design of management initiatives because the response of fishers to policy can then be predicted more accurately (Béné and Tewfik 2001; Gelcich et al. 2005). For example, in the case of the Anguillian fishery, crayfish hand-catchers were identified as primary exploiters because of their ability and motivation for profit. Any management option that curtails fishing opportunities will therefore have a larger impact on these individuals. Given that they also tended to be re-

spected individuals in the community, their opinion may influence that of other fishers. Participatory management could be targeted toward these individuals, using their individual skills and qualities for supporting conservation or sustainable harvesting initiatives. In addition, given that community participation is considered to be a key element for sustainable reef management (Friedlander et al. 2003; Martin-Smith et al. 2004; Springer 2006) and that fisher perception of not being included can lead to noncompliance, a clear understanding of fisher behaviour by managers is beneficial to all stakeholders (Kaplan 1998).

Knowledge of fishing grounds

Anguillian fishers appeared to demonstrate imperfect knowledge of the resources held at each site in two ways. Firstly, fish trap fishers did not position their traps at the sites of highest fish abundance. It is possible that fishers do not appear to be distributed according to fish abundance because our snapshot abundance estimates were made 1 year prior to the collection of fishing information and there was temporal variation in fish abundances. Seasonal differences in fish abundances resulting from spawning migrations or recruitment patterns (Letourneur 1996) were minimised by recording fish abundance and fishing data during the same season (i.e., both in spring). Interannual variation in the relative abundance of fish at each site was also unlikely to have masked any relationship between fishing pressure and resource distribution as we found a strong and significant correlation between abundance of fish at two sampling depths at four sites in 2003 and 2004 (Spearman's $R_s = 0.833$, $n = 8$, $P = 0.01$). This indicates that the relative profitability of sites to fishers is consistent between years. It is possible, however, that changes in fish abundances do occur (on longer and (or) shorter time scales than seasonal to annual) and that there is a lag before such changes are detected by fishers, who then initiate movements to and from sites. This may explain the observed high number of traps at some sites with low fish abundance (e.g., sites 2, 5, and 16) and the observed low number of traps at sites with high fish abundance (e.g., site 4). Interestingly, there were no sites with high numbers of traps and high fish abundance (K. Abernethy, personal observation). If this situation occurs only briefly as a result of rapid harvesting, it could have been missed in the snapshot. A cycling effect of fishing pressure and fish abundance may therefore exist that would be consistent with the IFD but impossible to capture in a snapshot study.

The second line of evidence suggesting imperfect knowledge of resource distribution by fishers lies in the changing accuracy of abundance perception with distance from port. Anguillian fishers using all methods estimated more accurately resource abundance at sites closer to the harbour, possibly because information about these sites was more forthcoming within the community and (or) because the sites were visited more frequently. Interviews revealed that some fishers were faithful to particular sites where they felt their catch was sufficient to meet their needs. This comment was often mentioned alongside time and cost constraints and applied to sites that tended to be closer to harbour. Therefore Anguillian fishers may not explore and thereby gain good knowledge of alternative sites.

Another reason for the apparent imperfect knowledge of fishers may be the high variation in individual PPUE observed. This variation could make it difficult for an individual to detect trends in fish abundance. Therefore, fishers may be acting in a risk-averse manner and fishing in areas where they can achieve an expected minimum yield (Oostenbrugge et al. 2001; Pet-Soede et al. 2001).

Understanding fisher knowledge could help managers predict the level of conflict with fishers that may arise, for example, from creating a no-take MPA within certain fishing grounds. Support may be higher if closed areas are perceived to hold relatively limited abundance of target species. The ability to predict fisher response could mean that a negative response may be mitigated and limited management funds could be used more effectively.

The IFD as a framework for understanding fisher behaviour

This study has shown that through testing the key assumptions of the IFD model and understanding the causes of violations of those assumptions, the IFD can provide a useful framework within which to gain detailed insights into the complexity and dynamics of a fishery. This approach facilitated a rapid appraisal of an important and often overlooked stakeholder group: fishers who depend on the reef ecosystem for goods and services. The identification of key resource users, patterns of depletion, and limitations of fishers, alongside economic and ecological data, is essential for effective and efficient development of management practices (Seijo et al. 1998). However, holistic investigations into fisheries generally require one or more years of intensive study prior to the formulation of a strategy (Alcala 1988; Friedlander et al. 2003; Martin-Smith et al. 2004). Given the current rate of coral reef degradation (Gardner et al. 2003; Wilkinson 2004), a rapid and accurate appraisal method could be a useful starting point. The IFD framework offers such a means of assessment and may therefore be of considerable use to policy makers.

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