Relationship between small-scale catch-per-unit-effort and abundance in New Zealand abalone (pāua, *Haliotis iris*) fisheries

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ABSTRACT

Catch-per-unit-effort (CPUE) is commonly used as an index of abundance in fishery stock assessments, but CPUE may be misleading, as a number of global fishery collapses have been attributed to a hyper-stable CPUE. In abalone (Halitidae family) fisheries, CPUE at large spatial scales may be hyper-stable because of aggregating behaviour and serial-depletion, whereby fishers sequentially fish areas with no corresponding decline in CPUE. Obtaining detailed spatial information in abalone fisheries might mitigate this problem, allowing CPUE to be used more confidently in these fisheries. Here, we report on the use of newly-developed high-resolution Global Positioning System (GPS) data loggers in New Zealand's blacklip abalone (pāua, *Haliotis iris*) fisheries. Using these data loggers, we tested, via a fish-down experiment, if CPUE is a reliable indicator of abundance at a small spatial scale and over a period of months. In the experiment, hyper-stability at small spatial scales occurred at high abundance, but CPUE reflected the estimated depletion level at the end of experimental fishing. This experiment suggests that the GPS data loggers provide a promising avenue to track CPUE at a small spatial scale, and to assess spatial resource use in New Zealand's pāua fisheries.

Keywords: pāua, abalone, catch-per-unit-effort, catchability, sustainable fisheries, spatial management

INTRODUCTION

Catch-per-unit-effort (CPUE) is often an important—and sometimes the only—index of abundance in fishery stock assessments. Nevertheless, a large body of research suggests that CPUE may be hyper-stable, underestimating declines in abundance (Harley, Myers, and Dunn, 2001). Furthermore, CPUE is strongly dependent on spatial patterns of fisheries and their resource (Hilborn and Walters, 1992; Prince and Hilborn, 1998; Walters, 2003; Ye and Dennis, 2009), which can distort the relationship between CPUE and abundance.

Hyper-stability in CPUE results from increased catchability of target species at low abundance. This increased catchability can be due to fisher behaviour, technology, as well as the biology and behaviour of the target species (Hilborn and Walters, 1992; Rose and Kulka, 1999). In addition, serial depletion, whereby fishers successively deplete local populations, may lead to hyper-stable CPUE. It disproportionately affects target species that disperse slowly relative to movements of the fishing fleet (Prince and Hilborn, 1998). Hyper-stability is considered to have been the cause of a number of invertebrate population declines that went undetected before stocks fully collapsed (Karpov et al., 2000; Kirby, 2004; Orensanz et al., 1998).

Globally, a range of abalone stocks have collapsed due to excessive fishing pressure that was incompatible with the biology of the stocks (e.g., Hobday, Tegner, and Haaker, 2000; Karpov et al., 2000; Woodby, Larson, and Rumble, 2000). While the management of abalone fisheries often operates at large spatial scales, abalone populations are spatially structured over considerably smaller scales (kilometres or less) (McShane, Black, and Smith, 1988; Prince and Hilborn, 1998) due to limited larval dispersal from local populations (McShane, Black, and Smith, 1988) and variation in their habitat. As a consequence, life-history parameters that are relevant to the fishery, such as growth and size-at-maturity, may also vary systematically at sub-kilometre scales (McShane and Naylor, 1995). The discrepancy between the spatial scale of abalone populations relative to that of fishery and management areas makes these populations particularly prone to serial depletion. In addition to low displacement and dispersion rates, the aggregating behaviour of abalone following fishing is considered to lead to hyper-stable CPUE. For this reason, it is important that CPUE data are obtained on the spatial scale of the resource to form the basis of an effective monitoring tool (Prince and Hilborn, 1998).

In New Zealand, blacklip abalone (pāua, *Haliotis iris*) are among the most valuable seafood resources, fished by free-diving fishers. In the following, we use the term "abalone" when we refer to fisheries of abalone within the genus *Haliotis* (or, equivalently, the family Haliotidae), and use the term "pāua" when we refer to *Haliotis iris* in New Zealand's fisheries. In pāua stock assessments, the primary indicator of stock abundance has been fishery-dependent CPUE data (Breen and Smith, 2008; Fu, 2012; Fu, McKenzie, and Naylor, 2012). Currently, these CPUE data are collected at relatively coarse spatial scales (10s of km) and standardised at larger scales (100s of km) every three years in preparation for stock assessments. Given the potential for hyper-stable CPUE, there is an obvious need to assure the reliability of CPUE as an abundance index.

To record catch and effort data at a scale close to that of pāua populations, Global Positioning System (GPS) data loggers were introduced into New Zealand's pāua fishery in 2010. The development of these dive loggers followed the introduction of similar units in the Tasmanian abalone fishery (Mundy, 2012). In the latter fishery, the data loggers provided an unprecedented resolution of the fishery data, allowing a detailed spatial analysis of diver data. This detailed analysis revealed valuable information on "hot spots" of fishing activity and patterns of resource use.

In addition to providing an improved qualitative understanding of the fishery, recent reviews (Mc-Cluskey and Lewison, 2008) and analyses (e.g., Hanchet, Blackwell, and Dunn, 2005; Mills et al., 2007; Murray et al., 2013) suggest that fishing data collected at fine spatial and temporal scales can substantially improve effort calculation and resulting CPUE indices. The temporal and spatial resolution of the data loggers make it possible, in theory, to test the hypothesis that divers adjust their fishing behaviour and spatial resource use to maintain high average catch rates in spite of declines in the resource. This adjustment may involve expanding fishing effort into previously unfished areas, or increasing dive depth and bottom times (i.e., time spent fishing at depth). These factors could be considered as additional effort being expended beyond the baseline effort of standard fishing, and are a form of effort creep that would not be detectable from basic effort measures alone (Marchal et al., 2006, 2001).

Here, we report on the development and experimental testing of CPUE data from data loggers to monitor pāua abundance in New Zealand's fishery. Using data from a fish-down experiment, we tested the relationship between effort metrics derived from data loggers and pāua biomass, and assessed the estimated CPUE index for hyper-stability.

METHODS

Study system

Pāua are fished throughout New Zealand by fishers free-diving for the resource, and the fishery is managed under the New Zealand Quota Management System (QMS). Within designated Quota Management Areas (QMAs), minimal legal size and a Total Allowable Commercial Catch are two of a number of management tools used to manage New Zealand's pāua fishery (e.g., Ministry for Primary Industries, 2012). Analysis of CPUE data for stock assessments currently relies on information from Pāua Catch Effort Landing Return (PCELR) forms, on which daily fishing time and catch per diver are recorded. Data from these forms are recorded in pāua statistical areas, which are subdivisions of the larger QMAs, and generally involve tens of kilometres of coastline.

Logger data

The data loggers used in the current study consisted of two compact units, a boat logger and a dive logger (also called "turtle logger") (Figure 1). The boat logger records catch, whereas the turtle logger records effort data. The turtle logger contains a Global Positioning System (GPS) unit, and is carried by divers in a pouch on the back of their wetsuits. These loggers record the position of the diver at the surface (here at 10-s intervals), and the depth of the diver during dive events (at 1-s intervals). The unit is automatically activated once it is submersed, and switches into dive mode when it is underwater at depth. Information about the catch is recorded using a second GPS unit (the boat logger), which captures the position of each landed catch bag of pāua, and also information on the daily catch by each diver.



Figure 1. Data loggers used in the current study to record catch and effort data in New Zealand's abalone (pāua, *Haliotis iris*) fishery. The data loggers include a larger boat unit (including buttons for recording catch bags, and a key pad for entering catch weight and other data) and a smaller, dive (or "turtle") logger that is carried by free divers, and records their position and dive depth (Image by E. Abraham).

The two units combined are referred to as pāua data loggers. Records from both units are needed to calculate CPUE. To collect these fishing data, divers enter a personalised identification number (henceforth "diver ID") in the boat unit and the number of their turtle logger (the "turtle ID"). The turtle ID then links the turtle logger data to the boat data, and the diver ID attributes the data to a diver.

Initial survey and fish-down experiment

To help develop methods for interpreting the pāua logger data, a fish-down experiment was carried out involving a previously unfished site in the outer Marlborough Sounds region of New Zealand, within pāua fishery management area PAU7 QMA (Figure 2). The experiment was conducted in the summer of 2011–12, and included an unfished site and an adjacent, fished site that was used as a control. During the fish-down experiment, a designated area at the unfished site was repeatedly fished by commercial pāua divers, until CPUE was reduced to levels similar to that at the control site that was also fished. During the experiment, pāua loggers were used to monitor changes in CPUE over a wide range of pāua abundance.

The unfished site was within Fighting Bay, which was closed to all fishing in 1996 to protect an undersea cable, and considered to have high pāua abundance. The control site was in a bay known locally as "Boat Harbour". This site was chosen because it was close to Fighting Bay, had a similar aspect, and was known to support commercial fishing for pāua. Both sites had a steep coast, with a shallow sub-tidal reef extending to a sandy bottom at between 10 and 15 m depth.

Before the fish-down experiment, a systematic survey of the two sites was carried out by scientific divers (on 2, 3, and 10 December 2011). During the initial survey at both sites, divers used approximately evenly-spaced lead-line transects (initially 50 m length, subsequently replaced with an 80 m line during the survey to allow it to extend to deeper water). The transects were placed using a boat, so that the positioning of the transect lines was not determined by the divers. Following placement, one diver swam along each transect line, allowing for more than one transect line to be surveyed at the same time. All pāua within 50 cm either side of the transect line were counted and measured (full shell length), using underwater, electronic callipers (Zebratech, Nelson). At the same time, the habitat was qualitatively classified into six different types based on bottom type and algal community. Habitat types were recorded at 2-m intervals using the callipers' data entry function. These data were used to provide an initial estimate of pāua abundance and habitat properties. The callipers also recorded the depth when data where recorded, providing the depth of the transect line and, therefore, the depth of each site.

Following the initial survey, a small area of coast of between 300 and 400 m length was selected on the south-western side of Fighting Bay (within the protected area) for the fish-down experiment. The area was naturally bounded on the western side by a sandy bay, and on the eastern side by a steep headland that fell quickly to the bottom. These features, together with the sandy floor of the bay, formed a naturally enclosed area. Using data from the initial survey, this area was estimated to contain between 7 and 13 t



Figure 2. Location of the fish-down experiment of New Zealand abalone (pāua, *Haliotis iris*), including the fish-down site within Fighting Bay (blue), and the adjacent, control site in Boat Harbour (orange).

of legal-sized (>125 mm shell length) pāua, depending on the estimation method used. Pāua were not expected to move in or out of the fish-down site during the experiment.

At Boat Harbour, pāua densities were lower, and an approximately 800 m length of coast was chosen as this control site. The area was marked by a small bay with a sandy beach at the northern end and a prominent rock to the south. Because of the length of coastline of this area, no substantial migration of pāua was expected to occur across its boundaries during the experiment.

The fish-down experiment was carried out on several days over the (austral) summer, between December 2011 and February 2012 (14 and 15 December 2011, 12 January 2012, 1 and 23 February 2012). At Fighting Bay, fishing was carried out every day of the experiment, whereas at Boat Harbour, it was on three days only (14 December 2011, and 1 and 23 February 2012). After the initial pass through the fish-down area in December 2011, fishing days were spaced out to allow remaining pāua to re-aggregate.

Pāua fishing

At both sites, pāua fishing was carried out by commercial free divers, using standard fishing methods. All pāua were collected as part of the fisher's Annual Catch Entitlement (ACE). No instructions were given to the divers on how to fish, beyond defining the areas. The fishing crew consisted of a skipper, four divers, a dive support person (or boating assistant), and deck hands that were responsible for measuring and storing the catch. Two vessels were used, a larger vessel and a small inflatable with outboard motor as a dive support vessel. There were four commercial pāua divers in the experiment. These divers are here referred to as divers A, B, C, and D.

Pāua were fished by free diving, using a flat tool to lever them off the rocks. The pāua were collected into catch bags that were able to hold up to 50 kg of catch. The catch bags were collected by the dive support person in the inflatable, and then transferred to the main vessel. As part of the experiment, each bag was weighed when it was landed on the main vessel. The bags were then emptied onto a sorting table, and the size of all pāua was assessed. Legal-sized pāua were stacked in bins, with each diver's catch being sorted into different coloured bins. At the end of the day, or when the vessel moved between sites, the bins were counted, the wet weight of the catch by each diver was estimated and recorded in the boat

logger and on the PCELR forms. Particular care was taken to keep the catch of each diver separate, as the divers were paid based on their individual catch. This payment structure motivates divers to maximise their individual catches.

Data preparation

The dive and boat logger position data were not always accurate. It was subsequently found that there was an internal compression error in the processing of the GPS data, which introduced a spurious offset onto some records (caused by dropping zeros where they occurred in decimals). This error could not be corrected for data collected during the fish-down experiment, but was corrected with a firmware fix later in 2012 (i.e., after the experiment had ended). Furthermore, as many of the surface intervals were short (less than 30 s), GPS positions were not always obtained. The position data from the dive loggers were prepared by fitting a running mean filter to the GPS data, with a total window length of 4 minutes. Positions that were more than 100 m distant from the running mean, or that were missing, were assumed to be errors, and were replaced with the running mean position. Boat logger positions were not prepared in this way.

Extracting effort metrics from data loggers

Data were downloaded from the turtle logger and boat unit as separate files, which were uploaded to a PostgreSQL database. Records from the boat unit were matched with dive records (from the turtle logger) within the database. For each day's fishing, we had records of all dives, landed bags, and start and end positions of all dives and bags. Meta-data on the day's diving, including fishing conditions (recorded as swell height and visibility, both in m) and the use of a boating assistant, was archived in the database.

Based on dive and bag landing data, we extracted three main effort metrics: i) the total fishing time, defined as the sum of half-hour intervals during which catch bags were landed (i.e., during which bag landing buttons were pressed on the boat unit); ii) the bottom time, defined as the time spent below the surface; and iii) the cumulative depth corresponding with the cumulative sum of median dive depths.

Relating fish-down CPUE to biomass

Using a Leslie depletion methodology (Leslie and Davis, 1939), we investigated how the three effort measures (total fishing time, bottom time and cumulative depth) related to surveyed biomass: if during an interval, *t*, there was a fishing effort, f_t , that resulted in a catch, C_t , then the CPUE over that interval was C_t/f_t . If it is assumed that the CPUE during the experiment was proportional to available biomass, B_t , then:

$$\frac{C_t}{f_t} = qB_t,\tag{1}$$

where q, is the catchability, defined as the proportion of the biomass that is removed through a unit of fishing effort.

In a fish-down experiment, it is assumed that the biomass remaining at time t is the initial population, B_0 , less cumulative catch until that point. For this assumption to be satisfied, it is required that there is no movement of animals in or out of the fish-down area for the duration for the experiment, and that the increase in the biomass from growth is small relative to the biomass at the start of the fish-down experiment. With this assumption, Equation 1 may be used to estimate the catch during the interval t:

$$C_t = f_t q(B_0 - \sum_{\tau=1}^{t-1} C_{\tau}),$$
(2)

with $\sum_{\tau=1}^{t-1} C_{\tau} = 0$ at t = 1.

By fitting this linear equation to the data, the catchability q and the original biomass B_0 within the fish-down area may both be estimated. In the analysis of the Fighting Bay fish-down experiment, a separate pāua catchability was estimated for each diver. The depletion equation was generalised so that for each diver i in a time interval t, the catch is

$$C_{i,t} = f_{i,t}q_i(B_0 - \sum_i \sum_{\tau=1}^{t-1} C_{i,\tau}).$$
(3)

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In applying the depletion equation to the Fighting Bay data, the time interval was taken to be a day's fishing as this time scale corresponds with the period of time at which catch is reported in the commercial fishery. Effort was taken to be one of the effort measures described above (i.e., we fitted one model per effort measure), and a combination of the three effort measures (i.e., a combined model; see below). The cumulative catch was calculated for each day by summing the estimated weight from all the bags landed by all divers on that day.

A Bayesian linear mixed model was used to fit Equation 3 to the fish-down experiment data for each of the three effort measures. The daily catches were assumed to be log-normally distributed, with variance θ and mean $\mu_{d,t}$, the latter defined by the logarithm of Equation 3:

$$\mu_{i,t} = \log(f_{i,t}) + \log(q_i) + \log(B_0 - \sum_i \sum_{\tau=1}^{t-1} C_{i,\tau}).$$
(4)

To test if bottom time and dive depth predicted catches at equivalent fishing time (i.e., to assess if effort was better described by a combination of effort variables), we added a regression term βX to the model in Equation 4, such that:

$$\mu_{i,t} = \log(f_{i,t}) + \log(q_i) + \beta X_{i,t} + \log(B_0 - \sum_i \sum_{\tau=1}^{t-1} C_{i,\tau}),$$
(5)

where β was a row-vector of regression coefficients and $X_{i,t}$ is a matrix with columns including the log of bottom time and cumulative depth effort measures, as well as an interaction term between bottom time and cumulative depth. The rationale for the last term was based on the consideration that bottom time is correlated with dive depth, and CPUE may thus vary as their product.

Lastly, we modified the depletion model to reflect a fishery context in which the real depletion level is unknown, and estimated a CPUE index I_t within the model:

$$\mu_{i,t} = \log(f_{i,t}) + \log(q_i) + \beta X_{i,t} + I_t.$$
(6)

All priors were chosen to be vague, but not uninformative. The initial population B_0 was given a gamma prior with mean 10 000 and rate 0.001, resulting in a standard deviation of 3160, which was considered sufficient to reflect uncertainty in survey estimates. The catchabilities, q_i , were given a hierarchical prior such that $logit(q_i)$ followed a normal distribution with mean μ_q and population variance τ_q estimated from a half-Cauchy prior with rate 0.01 (Gelman, 2006). All remaining priors (β and μ_q) were vaguely informative normal priors with mean zero and variance of 10 000.

Models were fitted using Markov Chain Monte Carlo methods within the software JAGS (Just Another Gibbs Sampler) (Plummer, 2013). The models were run for 1 000 000 iterations, following a burn-in of 20 000 iterations (see the JAGS code used to fit the model in Appendix A).

From the model, posterior distributions of the initial fishable pāua within the fish-down area and of the catchabilities for each diver were estimated. Model fit was assessed by comparing the actual daily catches with the estimated catches for each diver and day, obtained from samples of the posterior predictive distribution.

Similar models were deemed unsuited for the Boat Harbour site, since it was unclear whether other fishing crews had fished the site in-between survey dates. Data from Boat Harbour was thus used for qualitative comparisons only.

RESULTS

The scientific dive surveys prior to the fish-down experiment assessed the abundance and size distribution of New Zealand abalone (pāua, *Haliotis iris*) at Fighting Bay (closed to fishing since 1996) and adjacent Boat Harbour (open to fishing) in December 2011. Pāua length and depth data were obtained from eight weighted line transects within the experimental fish-down site at Fighting Bay, and from ten weighted line transects at Boat Harbour (data were also collected on transect lines outside the Fighting Bay fish-down area, but are not presented here) (see additional information about the survey results in Appendix B).

At the start of the fish-down experiment at Fighting Bay (14 and 15 December 2011), it took two days for the commercial pāua divers to fully cover the fish-down area. On the second and third visits, it took a

day each to cover the fish-down area, and on the final visit, two full sweeps of the fish-down area were made in a single day.

Over the five days, there was a total of 7950 kg (greenweight) pāua taken from the previously unfished site at Fighting Bay (Table 1). At the fished site, Boat Harbour, 550 kg of pāua were collected over three days. Over the course of the experiment, total catches within the Fighting Bay area decreased, whereas they remained relatively similar at Boat Harbour.

Of the four divers participating in the experiment, two divers (A and B) collected pāua every day; one diver (C) collected pāua on four days, but was unable to fish on the final day; and one diver (D) joined the experiment for the final two days. With the exception of diver D on 1 February 2012 (who started later than the other divers that day), all divers were able to fish for the same length of time each day. Throughout the experiment, diver A had a consistently higher daily catch at each site than the other divers.

Table 1. Total greenweight (kg) of abalone (pāua, *Haliotis iris*) collected at two sites during the fish-down experiment in New Zealand, summarised by day and by diver, from boat logger data. Fighting Bay was closed to fishing in 1996, whereas Boat Harbour was open to fishing.

(a) Fighting Bay					(b) Boat Harbour						
Date	Diver				Total	Date	Diver _{To}				Total
	А	В	С	D		Dute	А	В	С	D	iotui
2011-12-14	735	585	620		1940	2011-12-14	50	35	30		115
2011-12-15	850	705	690		2245	2012-02-01	75	50	45	40	210
2012-01-12	635	510	565		1710	2012-02-23	85	70		70	225
2012-02-01 2012-02-23	430 340	400 190	280	220 195	1330 725	Total	210	155	75	110	550
Total	2990	2390	2155	415	7950						

Fishing effort was recorded on PCELR forms as time spent in the water. Total time (by all divers) at the Fighting Bay site ranged from 21.0 to 39.5 h per day (??), while at Boat Harbour, the total time ranged from 10.0 to 14.0 h. On each day and at each site, records showed that each diver spent the same time fishing, with the exception of 1 February 2012 at Fighting Bay. On this day, records showed that divers A, B, and C were fishing for 10.5 h, whereas diver D spent 8.0 h fishing.

Fishing patterns

In total, there were 6895 dives recorded during the experiment, but not all dives were recorded (Appendix C, Table C-1). Dive records were incomplete as the turtle loggers used by two divers failed to switch on when the divers re-commenced fishing after a break, owing to an unreliable seawater switch. For diver B, the switch did not operate correctly on the first three days of the fish-down experiment, so that only partial data were recorded. The unit used by diver A failed to record data for most of the fishing on 12 January 2012.

For all divers, the depth loggers on the units collected data. Four turtle units had GPS positions for between 96.9% and 99.6% of all dives. For one unit, however, the GPS unit did not routinely acquire a position while it was at the surface. For this unit (used by diver C), locations were only obtained for 43.4% of all dives. After the first three days of the experiment (14 and 15 December 2011, and 12 January 2012) the unit was replaced. The new unit reliably collected position data.

Although the missing data meant that dive positions were incomplete, changes in the dive behaviour were evident as the experiment proceeded. During the initial two days, the divers fished methodically as a group in Fighting Bay, first focusing on the western and then the eastern area (Figure 3(a)). On the first day, all divers targeted pāua in the densest patch in the western area, staying close to each other and fishing systematically. On the second day, the divers fished the eastern half of the area for the first time, also staying close to each other. As pāua density decreased on subsequent dates of the experiment, the divers separated and fished relatively independently of each other. This pattern was particularly evident on 1 February 2012, when each diver fished individually in distinct areas of the bay. On the final day of the fish-down experiment, two full searches by three divers (A, B, and D) were made through of the bay. On the final day of the fish-down experiment, two full searches over the whole Bay were made by three

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(a) Fighting Bay

Figure 3. Positions of commercial divers (A–D), fishing for abalone (pāua, *Haliotis iris*) at two sites during the fish-down experiment in New Zealand, for each day of fishing. Fighting Bay was closed to fishing in 1996, whereas Boat Harbour remained open to fishing and was used as a control site. The points are (running mean-) adjusted positions from Global Positioning System data, recorded at the start of each dive. Land is indicated in grey.

divers (A, B, and D) for any remaining pāua. At Boat Harbour, the divers fished independently on all three fishing days, and this pattern was particularly clear on 23 February 2012 (Figure 3(b)).

Over the five days of fishing in Fighting Bay, there were 5098 dives that were longer than 5 s. The

average duration of all dives was 15 s, and the average duration of dives that were longer than 5 s was 19 s (Figure 4). Most dives (around 99%) were less than 60 s long, with 95% of all dives lasting less than 37 s. There was no indication of any change in dive duration over the course of the fish-down experiment. Divers A and B tended to make longer dives, while diver C made shorter dives, and this pattern was consistent throughout the experiment.



Figure 4. Duration of dives (s) for each of four abalone (pāua, *Haliotis iris*) divers A–D on each day of the fish-down experiment at Fighting Bay, New Zealand in 2011–12. Fighting Bay was closed to fishing in 1996.

The dives were shallow, and the average depth of dives longer than 5 s was 1.7 m. Of all dives, 95% had a maximum depth of less than 3.6 m, and there was only one maximum depth that exceeded 10 m. There were no short, deep dives, reflecting the time needed to descend and ascend (Appendix C, Figure C-1). This time was around 5 additional seconds for every additional metre of depth (for this reason, an interaction terms was included in standardisation models, see below).

At Fighting Bay, the median catch-weighted depth was 1.4 (95% c.i.: 0.5 to 5.2) m (Figure 5). At Boat Harbour, the catch was deeper, with a median catch-weighted depth of 1.6 (95% c.i.: 0.5 to 4.1) m. The median depths were shallower than the median depths of pāua found during the survey (Appendix B, Figure B-1), although the catch depths were not corrected for tidal height.

The median proportion of the time fishing that divers spent underwater was 29.5 (IQR: 23.8 to 31.9) % (Appendix C, Figure C-2). There were consistent differences between divers. For example, diver C (the oldest diver) spent consistently the least of the fishing time underwater, whereas diver D (the youngest diver) recorded the highest percentage of time underwater. The proportion of time underwater varied from day to day, but was typically similar for divers at Boat Harbour and at Fighting Bay on the same day. This ratio appeared to be primarily determined by diver behaviour and possibly by sea conditions (which were similar between Boat Harbour and Fighting Bay on the same day).

Catch patterns

The catch in Fighting Bay was concentrated in a small area (Figure 6). Because of missing dive data from the turtle loggers, only 64% and 87% of the catch was spatially located at Fighting Bay and Boat Harbour, respectively. Despite these missing data, the maximum amount of pāua fished per unit area at Fighting Bay was 221 kg from an area of only 0.01 ha (100 m^2). The catch was highly concentrated: although the dives recorded by the GPS covered an area of 3 ha, 50% of the catch came from an area of only 0.23 ha, and 80% of the catch was from an area of 0.6 ha. In absolute terms, the catch from 1 ha of the areas with the highest catches was 4635 kg. Because of the catch that was not spatially located, the actual yield from this area would have been higher.

In contrast, at the fished site at Boat Harbour, the maximum catch per 0.01 ha was only 11 kg of pāua. The relative concentration of the catch was similar to that at Fighting Bay, with 50% of the catch from an area of only 0.53 ha, and 80% of the catch from an area of 1.5 ha. In absolute terms, however, the catch from 1 ha with the highest catches was 327 kg. This catch reflected 7% of the catch from the same-size area at Fighting Bay (even though the effort in these areas was distinctly different).

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Figure 5. Relative distribution of abalone (pāua, *Haliotis iris*) catch with depth for each day of the fish-down experiment at two sites in New Zealand. Fighting Bay was closed to fishing in 1996, whereas Boat Harbour remained open to fishing and was used as a control site. The density of catch by dive depths was calculated in 0.5-m depth bins. Depths are raw data and were not corrected for tidal height.

These statistics are likely to be affected both by the missing data, and by scatter in the GPS positions. The scatter tends to increase the area that has apparently been fished, and causes a larger number of apparent cells with small catches. This effect makes the catch appear to be more relatively concentrated than it may actually be. Other limitations for comparing total catches from Boat Harbour and Fighting Bay are due to the markedly different fishing effort between the two sites. In addition, there may have been growth of pāua during the season, and Boat Harbour may have also been fished by other divers than those involved in the experiment.

Another aspect evident from the data was that the fishing was size-selective (Appendix D). At the beginning of the experiment, divers selected pāua that were above the legal size without having to measure them. On the first day of the fish-down experiment, only 2.7% of the shells had a basal length less than 130 mm. As the experiment progressed, the divers were more thorough, there were fewer large pāua available, and the proportion of shells less than 130 mm increased tenfold to 28.8%. Over the course of the experiment, the proportion of shells larger than 140 mm decreased from around three-quarters to around one-quarter.

Catch-per-unit-effort

For the three measures of fishing effort, total fishing time, bottom time, and cumulative depth, there was a decreasing degree of association between cumulative catch and CPUE for fishing in Fighting Bay (Figure 7). After a plateau in catch rates for the first two days, there was a relatively linear relationship between CPUE and cumulative catch for total fishing time, with CPUE for all four divers tightly clustered along this trend. For bottom time, there was greater scatter around the relationship between CPUE and cumulative take for the initial three days of the experiment, with less scatter and a more obvious decline in CPUE on the last two days. The effort measured by cumulative median depth showed a similarly scattered pattern on the first days, followed by a linear decline in CPUE.

Using the proportion of bottom time or the cumulative median depths as effort measures, the CPUE on the final day at Fighting Bay approached the CPUE at Boat Harbour (Figure 7, Tables C-3 to C-5). Using

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(a) Catch density at Fighting Bay

(b) Catch density at Boat Harbour

Figure 6. Total amount of abalone (pāua, *Haliotis iris*) fished per unit area from recorded dives during the fish-down experiment at two sites in New Zealand. Fighting Bay (a) was closed to fishing in 1996, whereas Boat Harbour (b) remained open to fishing and was used as a control site. For each site, the amount is shown in $10\text{-m} \times 10\text{-m}$ areas (i.e., 0.01 ha each). In (a) cells with less than 2 kg of pāua are not shown. At Fighting Bay and Boat Harbour, respectively, 64 and 87% of the catch was spatially located. Also shown is the cumulative catch per area for each site (c).



Figure 7. Relationship between cumulative catch and daily catch-per-unit-effort (CPUE) of abalone (pāua, *Haliotis iris*) during the fish-down experiment at two sites in New Zealand in 2011–12. Fighting Bay was closed to fishing in 1996, whereas Boat Harbour remained open to fishing and was used as a control site. Fishing effort per commercial pāua diver (A-D) was measured by total fishing time based on data from dive data loggers, fishing time measured as bottom time, and cumulative median depth of dives.

total time as a measure, the CPUE at Boat Harbour was less than the CPUE at the end of the Fighting Bay fish-down experiment. For all measures, CPUE at Boat Harbour seemed to be increasing over the course of the experiment.

The depletion model produced good fits to the data, with the goodness-of-fit for the three effort types mirroring the scatter in raw CPUE around the linear decline (Figure 8). The model with total effort and dive effort added as covariates produced the best fit to the data (i.e., Equation 5), with a total log-likelihood of 4.3 versus 3.2, -9.05 and -13.25 for models with total time, bottom time and cumulative depth as sole effort variables, respectively. For the best fitting model (Equation 5), B_0 was estimated with a posterior mean of 9973 kg (95% c.i.: 9022 - 11539 kg; Table 2). This finding suggests a posterior mean depletion level of approximately 20% of B_0 . All models produced similar estimates for B_0 , with a range from 8800 to 10800 for posterior medians from different models, which was within the confidence limits of the model given by Equation 5.

The regression coefficients for dive parameters (cumulative depth and bottom time) suggested that neither cumulative depth nor bottom time had strong effects for average dive events (Table 2). While depth was not a significant factor in this model, the probability of cumulative depth being associated with higher CPUE was around 85%. The interaction of depth and bottom time was positive, indicating that with greater cumulative depth, the effect of bottom time became more positive. These dive effort variables seemed to primarily affect CPUE at lower abundance, as the scatter of observed versus predicted catches at high catches was similar between a model with total time only (Figure 8(a)) and the model with all effort variables (Figure 8(d)). Only for lower catches (i.e., for the last two days of the experiment) do the effort variables reduce the deviation of predictions from observed data (Figures 7, 8).

The estimated CPUE index from Equation 6 closely mirrored the depletion estimated in the depletion model (Equation 5; Figure 9). The estimated index followed a slightly domed shape, suggesting some hyper-depletion, relative to the depletion estimated by the model. Nevertheless, the estimated depletion at any day remained well within the 95% confidence envelope of the model index. By the end of the experiment, there was close agreement between the estimated index and the depletion level estimated when taking into account actual removals.

DISCUSSION

CPUE is often seen as a problematic and sometimes profoundly misleading indicator of stock biomass in relatively immobile shellfish populations that are prone to serial depletion (Karpov et al., 2000; Prince and Próo, 1993). The fish-down experiment presented in this study suggests that CPUE measured at

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Figure 8. Observed versus predicted catch of abalone (pāua, *Haliotis iris*) for the depletion model (see Equation 4) used in the fish-down experiment at Fighting Bay, New Zealand. Fishing effort, *f*, in the model was (a) total fishing time, (b) bottom time, or (c) cumulative depth of commercial pāua divers (A–D). Panel (d) shows the fit of the model with total dive effort and total time added as covariates (see Equation 5).

Table 2. Posterior summaries of estimated model parameters in the depletion model (see Equation 5) used in the fish-down experiment of New Zealand abalone (pāua, *Haliotis iris*). The model was applied to data collected from commercial pāua divers using dive data loggers. The estimated probability that the parameter is greater than zero was $P(\theta > 0)$.

Parameter	Summary statistic				
	Mean	$P(\theta > 0)$	2.5%	97.5%	
β , bottom time	-1.11	0.04	-2.47	0.17	
β , cumulative depth	0.03	0.54	-0.63	0.68	
β , cumulative depth \times bottom time	1.16	0.93	-0.48	2.90	
Catchability, q	0.017	1	0.0099	0.038	
Unfished biomass, B_0	9301	1	8563	10944	

appropriate spatial and temporal scales may still provide a satisfactory index of abundance trends in these fisheries. New technologies such as the data loggers presented here thus provide potential for small-scale stocks for which fishery-independent, scientific surveys are logistically and financially unfeasible, and CPUE remains the only available indicator of abundance trends.

By applying the depletion model in both a fishery-like context (i.e., without consideration of total removals from the area; Equation 6) and in the experimental context (Equation 4), we were able to show that the estimated abundance index in the fishery setting closely followed the estimated depletion from the experiment. The estimated index showed slight hyper-stability, but at levels close to fishery depletion and CPUE (i.e., those found at the control site), the index matched the estimated depletion closely. The decline of CPUE over the course of the fish-down experiment is consistent with a previous fish-down experiment in Tasmania (Prince, 1989), during which CPUE declined over the course of seven days of fishing on a previously closed reef. Nevertheless, the index estimated here described variation over orders of magnitude that are considerably greater than variations observed in pāua fisheries around most of New Zealand. Therefore, it remains to be shown whether the data-logger CPUE reflects biomass variation in a fishery context with as much accuracy as in the experimental setting.

The slight hyper-stability in both raw CPUE (see Figure 7) and the estimated index (see Figure 9) likely resulted from some serial depletion on a small scale over the course of the experiment. This depletion resulted from divers taking two days for a complete first pass of the area, selecting large pāua, and only systematically revisiting each area later in the experiment. The experimental data, therefore, support the concept of serial depletion for pāua fisheries. Nevertheless, it appears that a fishing event at a site does not remove sufficient biomass to cause local depletion (CPUE was still high on subsequent days). It is, therefore, unlikely that serial depletion would not be noticed and cause fishery collapses on its own as any subsequent visit to a previously fished area would reveal declines in biomass.

Other factors, such as aggregating behaviour and handling time are often thought to decouple CPUE from abundance in abalone (Hilborn and Walters, 1987; Prince, 1989). Handling time was likely the cause for the small scale serial depletion observed during the experiment: early in the experiment, pāua abundance was so high that only part of the bay could be fished in a single day. Handling time was thus synonymous with serial depletion, leading to the plateau in catch rates at high abundance during the first tow days of the experiment.

The duration of the Fighting Bay fishdown experiment (72 days) was chosen in part to allow for pāua to re-aggregate between fishing events. Such re-aggregation at low density can effectively increase catchability at low biomass and cause hyper-stability in the CPUE index (Dowling, Hall, and McGarvey, 2004a; Prince, 1989). Movement estimates for abalone in general, and for *H. rubra* are highly variable and habitat dependant (Prince, 1989; Shepherd, 1986), and whether the time between fishing events was sufficient to allow for aggregation thus remains unknown. However, given the clear spatial use pattern, serial depletion was a more likely explanation for the slight hyper-stability in estimated catch rates. Over greater temporal and spatial scales, the possibility of re-aggregation of pāua and resulting hyper-stability need to be considered when interpreting abalone CPUE. In a intermittently closed area (Waterloo Bay) in South Australia, annual CPUE did not reflect survey abundance over nearly five-fold changes in adult density (Dowling, Hall, and McGarvey, 2004a). The authors attributed this apparent decoupling



Figure 9. Canonical catch-per-unit-effort (CPUE) index (black solid line) estimated from a depletion model (see Equation 6) used in the fish-down experiment of New Zealand abalone (pāua, *Haliotis iris*). The model was applied to a fishery context in which the real depletion level is unknown. The x-axis shows the estimated depletion level on each day using the depletion model, whereas the y-axis quantifies the estimated canonical index. The dashed line is the 1:1 line (i.e., perfect agreement between "true" and estimated depletion level), the shaded area is the 95% confidence interval.

of abundance and CPUE to aggregating behaviour of abalone and targeted fishing on aggregations (Dowling, Hall, and McGarvey, 2004a,b). Nevertheless, some of the decoupling between CPUE and survey abundance in Waterloo Bay, South Australia, may have also been due to varying and potentially inaccurate dive survey methods. In New Zealand, dive surveys similar to those used in Waterloo Bay were discontinued after extensive simulation testing suggested that the dive survey indices frequently resulted in misleading biomass trends (Haist, 2010).

While it is difficult to assess whether CPUE on smaller spatial and temporal scales consistently leads to a closer relationship with biomass compared with annual, large-scale indices, the difficulty of relating CPUE on large spatial and temporal scales to abundance measures in abalone highlights the need for a more explicit spatial, temporal and management interpretation of abalone CPUE. For instance, with the advent of data loggers, CPUE could be split into spatial units, and estimation and CPUE trends should account for (i.e., impute) CPUE in areas that are unfished in the time interval used for the index (Walters, 2003). The pāua data loggers thus present an opportunity to obtain high-resolution effort data to monitor spatial use of the fishery and construct a monitoring programme that explicitly accounts for the spatial nature of the fishing activity. During the course of the experiment, catches were also recorded on a fine spatial scale, yet we chose to analyse the data at a day scale, since this approach reflects how catches are reported in the fishery. While it is preferable to obtain catch data and, therefore, CPUE at very fine spatial scales, this resolution of catch data is currently not feasible. Nevertheless, the detailed effort-reporting provides a spatial context that supplements CPUE trends, and should allow for the development of more sophisticated models that include spatial information in the calculation of CPUE indices (Shelton et al., 2014; Thorson and Ward, 2013; Ward et al., 2015).

If CPUE is a measure of available biomass at the scale investigated here, then the CPUE at Boat Harbour, similar to the CPUE on the final day at the fish-down site, suggests that abundance at the former site is low. Under the assumption that the carrying capacity per unit area at Boat Harbour is similar to that at Fighting Bay, a simple application of the results from Fighting Bay suggests a biomass level below 20% B_0 . This inference is supported by the increase of CPUE at the control site despite catch over the course of the experiment. This increase suggests that abundance at Boat Harbour is at a level at which growth over short time spans (leading to animals growing over the legal minimum catch length of 125 mm), drives

availability of catchable biomass.

Total fishing time provided the best fit to the data of any of the single-effort models. Nevertheless, all divers fished for nearly the same amounts of time, and the relationship was clearly driven by the strong signal of declining abundance. While diving and spatial fishing behaviour are a part of pāua fishing effort, it was difficult to separate their influences on CPUE, and their importance for CPUE analysis in this study. The possible correlation of cumulative depth with CPUE, as well as the strong interaction between cumulative depth and bottom time, indicate that dive effort influenced CPUE. The weak relationship of dive effort variables may have been driven by high availability of pāua at shallow depths (see ??). Nevertheless, in pāua fisheries around New Zealand, high abundance of pāua at shallow depths are most likely rare outside protected areas. The coordinated and systematic fishing during the first two days of the experiment may have further contributed to obscuring strong patterns in the influence of dive parameters on CPUE: only fishing on the last three days of the experiment reflected fisher behaviour seen at the control site (i.e., the spatial division of the fishing area). Low abundance of pāua in shallow areas and more spatially segregated fishing may lead to a greater importance of dive effort in the fishery. This hypothesis is supported by improvements of model fit in the depletion model with regression variables for the last few days of the experiment.

Although we focused on CPUE in the analysis of the fish-down data, the detailed spatial information that the data loggers provide will allow for more sophisticated analyses of spatial resource use in the future. In Tasmania, Australia, spatial information from abalone data loggers has been used to analyse shifts in fishing "hot spots" (Mundy, 2012). Similarly, the detailed dive information will allow for tracking of distributions of fishing depth and duration over time. In the fish-down experiment, the divers did not markedly shift their fishing depth as abundance decreased, but this behaviour may have been related to the distribution of catchable pāua. If the resource extends into deeper waters elsewhere, shifts to greater depth may indicate that more accessible parts of the resource are depleted (Prince and Hilborn, 1998). Additionally, the fish-down experiment showed a strong decline in mean shell length, and a shift in the length-frequency distribution of fished pāua. Shell length is used as an indicator of fishery health in South Australian abalone fisheries, and the New Zealand pāua industry routinely carries out shell sampling. It may thus be possible to use length-frequency data as an indicator for New Zealand pāua status.

ACKNOWLEDGMENTS

The development and deployment of the loggers is being managed by the fishing industry, through the Pāua Industry Council, supported by Seafood Innovations Limited and the Ministry for Primary Industries.

We are extremely grateful to the many passionate people who have helped with this work. Firstly, special thanks to Dave and Jason Baker and the fishers who carried out the fishing (Craig Perano, Barry Chandler, and Geoff Laing), and the other crew, for being so keen on improving the knowledge and understanding of the fishery. They were a pleasure to work with. The initial survey was organised by Nigel Keeley and Ellie Watts from Cawthron Institute, and we appreciate their willingness to help at short notice. Thanks are due to Transpower, Seaworks, and the crew of the SeaPatroller, for access to Fighting Bay, which is a special place through their careful stewardship.

The pāua logger project has depended on the innovation of John Radford from Zebratech (Nelson, New Zealand), and the preparation of this report depended on a number of people at Dragonfly who helped with the data processing, principally Marc Hasenbank and Finlay Thompson, whose willingness to wrestle data into shape is much appreciated.

Thanks also to the Ministry for Primary Industries staff (especially Julie Hills, Martin Cryer, and Allen Frazer) who supported the project through the delicate initial stages and are always looking ahead to the next steps. We also appreciate the continued encouragement from the Australian abalone researchers (especially Craig Mundy and Malcolm Haddon) who inspire with the progressive management of their fisheries.

Above all however, we wish to acknowledge the steady persistence of Jeremy Cooper and Storm Stanley of the Paua Industry Council, who have pursued the pāua logger programme since the beginning, and who have been supportive of this work throughout. The research was funded by Ministry for Primary Industries project PAU2010-03, with co-funding from Seafood Innovations Limited.

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