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Assessing the sublethal impacts of anthropogenic stressors on fish: An energy-budget approach

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Abstract

Fish are increasingly exposed to anthropogenic stressors from human developments and activities such as agriculture, urbanization, pollution and fishing. Lethal impacts of these stressors have been studied but the potential sublethal impacts, such as behavioural changes or reduced growth and reproduction, have often been overlooked. Unlike mortality, sublethal impacts are broad and difficult to quantify experimentally. As a result, sublethal impacts are often ignored in regulatory frameworks and management decisions. Building on established fish bioenergetic models, we present a general method for using the population consequences of disturbance framework to investigate how stressors influence ecologically relevant life processes of fish. We partition impact into the initial energetic cost of attempts to escape from the stressor, followed by the energetic impacts of any injury or behavioural change, and their consequent effects on life processes. As a case study, we assess the sublethal effects of catch and release angling for the European sea bass (*Dicentrachus labrax*, *Moronidae*), a popular target species for recreational fishers. The energy budget model described is not intended to replace existing experimental approaches but does provide a simple way to account for sublethal impacts in assessment of the impact of recreational fisheries and aid development of robust management approaches. There is potential to apply our energy budget approach to investigate a broad range of stressors and cumulative impacts for many fish species while also using individual-based models to estimate population-level impacts.

KEYWORDS

anthropogenic disturbances, catch and release angling, European sea bass (*Dicentrachus labrax*), population consequences of disturbance framework, recreational fisheries

1 | INTRODUCTION

With a rising human population and increasing global development, there is a worldwide intensification in the production of food, energy and resources with manifold effects on biodiversity and the environment (Vitousek, Mooney, Lubchenco, & Melillo, 1997). Aquatic ecosystems and their fish populations are under increasing pressure from stressors associated with these human activities (Gordon et al., 2018; Reid et al., 2019). The stressors that affect fish can be direct (e.g. exploitation via commercial and recreational fishing) and/or indirect (e.g. chemical pollution and anthropogenic noise), and consequences for fish range from mortality to more subtle sublethal effects on physiology or behaviour that impact fitness (Gordon et al., 2018; Lewin et al., 2019). Stressors can also interact in unpredictable and complex ways and may cause impacts that are greater than the sum of the individual stressors (Crain, Kroeker, & Halpern, 2008).

Where possible, sublethal effects should be documented experimentally. Experimental studies investigating the effects of stressors on fish include: anthropogenic noise (Popper & Hastings, 2009); pollution (Hamilton et al., 2016); climate (Cheung, Pinnegar, Merino, Jones, & Barange, 2012; Heath et al., 2012); commercial fishing (Cook et al., 2019); and recreational fishing (Bartholomew & Bohnsack, 2005; Lewin et al., 2019). Experimental approaches to investigate sublethal effects are mostly divided into containment, telemetry or mark-recapture studies (Ferter, Hartmann, Kleiven, Moland, & Olsen, 2015). Containment experiments keep live fish in a container, expose them to stressors, and observe their impacts. Containment gives direct access to all the study fish, but many species are not suited to be kept in cages (e.g. large or highly mobile and migratory species [Braun, Kaplan, Horodysky, & Llopiz, 2015; Horodysky, Cooke, Graves, & Brill, 2016]) and the effects of containment can obscure effects of the experimental stressor (Pollock & Pine, 2007). In telemetry studies, captured fish are tagged to record data on their behaviour after release (Donaldson, Arlinghaus, Hanson, & Cooke, 2008; Pollock & Pine, 2007) and often only fish in good condition are tagged due to the cost of tags and ethics (Brattey & Cadigan, 2004; Graves, Luckhurst, & Prince, 2002). Mark-recapture experiments are similar to telemetry but only use identification tags, requiring that the fish be recaptured, when its condition can be compared with the last time it was caught (Pollock & Pine, 2007). Both telemetry and mark-recapture have the advantage of taking place in the fish's natural environment but are often limited by difficulties tagging and following sufficient numbers of fish. In addition, stressor responses can be difficult to distinguish from the impacts of the surgery or tagging event (Ferter et al., 2015; Pollock & Pine, 2007). So while experimental studies have made important contributions to our understanding of stressors, there are often major logistical limitations to what can be achieved, especially considering the broad range of sublethal impacts, in contrast to mortality effects where the individual either survives or dies. Despite the challenges, it is important to understand all stress effects including sublethal effects if we are to recognize and mitigate our impact on global fish populations.

A complementary approach to investigate sublethal effects from human stressors is to use modelling. One important approach is the population consequences of disturbance framework (PCoD) (National Research Council, 2005). This framework was originally developed for marine mammals, but is broadly applicable and appropriate for most fish species (National Research Council, 2005). The effects of stressors are first quantified on individuals, where effects depend on the severity and duration of exposure which generally varies between individuals within a population. Effects of exposure eventually affect fitness traits—survival, fecundity and growth—and these in turn lead to effects on population dynamics. The success of this approach for marine mammals has been evaluated by Pirotta et al., 2018, who reviewed cases where the PCoD framework was used and the modelling methods that were available at each step from individual effects of stressor exposure through to population-level impacts. Here, we focus on the first stage of the PCoD framework, evaluating the sublethal effects of stressors on individual fish. Building on previous established bioenergetics modelling approaches (Beyers & Rice, 2002; Beyers, Rice, & Clements, 1999; Beyers, Rice, Clements, & Henry, 1999; Rice, 1990), we introduce a novel modelling approach that considers energy losses from both the initial escape and response to the stressors, not analysed in previous studies and longer-term reduction in energy intake due to injuries or behavioural change. To do this, we employ widely used fish energy budgets to calculate the effects of stressors on the fitness traits of growth and reproduction. The success of the energy budget approach derives from the similarities among fish in rates at which they can acquire energy from food and allocate it to vital processes. The same functional forms often well describe rates of energy uptake, maintenance (metabolism), growth and reproduction, and how they scale with body size and temperature (Clarke & Johnston, 1999; Peters, 1986; Sibly et al., 2013). If information is known, or can be assumed, about behavioural responses to stressors, this can be incorporated into an energy budget model. For example, if an individual exhibits avoidance behaviour such that it does not feed, the resultant effects on growth and reproduction can be modelled using an energy budget. In this way, certain physiological and behavioural responses to stressors can be evaluated simultaneously. This is useful because it is nearly impossible to separate behaviour and physiology when studying wild fish in the field (Cooke et al., 2014).

One example of a stressor with potentially appreciable sublethal effects is marine recreational fishing. Marine recreational fisheries are a high-participation activity with large economic and social benefits, but can also have significant impact on fish stocks (Cooke & Cowx, 2004; Hyder et al., 2018; Radford et al., 2018). As a result, recreational fisheries need to be incorporated into fisheries assessment and management (Arlinghaus et al., 2019; Hyder et al., 2018). Catch and release (C&R) fishing is the process of capturing a fish with a hook and line, and then releasing the live fish back into the water assuming that the fish will survive (Arlinghaus et al., 2007). C&R is an important tool for the management of recreational fisheries (Arlinghaus et al., 2007; Policansky, 2002). Global release rate has been estimated to be 60% in recreational fisheries, corresponding to about 30 billion released fish annually (Cooke & Cowx, 2004; Horodysky, Cooke, & Brill, 2015). Release rates have also been shown to be high in the European marine recreational fishery and are driven by regulatory (e.g. bag limits) and voluntary (e.g. conservation ethic) processes (Ferter et al., 2013). Hence, understanding the sublethal impacts of marine recreational fisheries is important for effective fisheries management. One good example is the European sea bass (*Dicentrachus labrax*, *Moronidae*). Sea bass is a valuable and important target species for commercial and recreational fisheries in Europe (Herfaut, Levrel, Thébaud, & Véron, 2013; Radford et al., 2018; Vázquez, Muñoz-Cueto, Pérez-Ruzafa, & Marcos, 2014), and assessments have shown a rapid decline in one important stock (northern sea bass) over the past decade attributed to a combination of poor recruitment and fishing mortality (ICES, 2018a). This has led to management measures since 2015 for both recreational and commercial fishers, including closed areas and seasons, an increase in the minimum landing size, and monthly bag and boat limits that all increase the numbers of fish being released (ICES, 2018a). Post-release mortality of recreationally caught sea bass is low (Lewin et al., 2018) and has been included in the assessment of northern sea bass (ICES, 2018b). However, no attempt has been made to assess the sublethal effects of C&R as the impacts on reproduction and growth are difficult to measure, despite the large numbers of fish that are being released.

The challenges with assessing sublethal effects of stressors experimentally, the lack of comprehensive modelling approaches, the increasing number and magnitude of stressors, and management decisions increasing the number of fish released, all mean that new approaches are needed to ensure sustainable exploitation of fish stocks. Here, we focus on the first stage of the PCoD framework, evaluating the sublethal effects of stressors on individuals. We introduce a modelling approach that uses energy budgets to calculate the effects of acute stressors on the fitness traits of growth and reproduction. We build on previous approaches and model the energetic costs of 1) escaping the stressors effects and 2) longer-term reduction in energy intake due to injuries or behavioural change. Reduced feeding results in reduced energy available for growth and reproduction, and so reduced fitness which is estimated using the model. We illustrate the potential use of this general model through an application to C&R fishing for sea bass in the UK.

2 | METHODS

2.1 | The energy budget model

An energy budget model was used to investigate the sublethal effects of anthropogenic stressors on fish. The energy budget model was implemented in R (version 3.4.3) (R Core Team, 2012). The total energetic cost of exposure to the stressor (C_T) is the sum of the energy required to escape from the stressor (C_E), for fish that attempt escape, and the energetic cost of injury or behavioural change caused by the stressor (C_I) (all units of energy are kJ):

$$C_T = C_E + C_I \tag{1}$$

The energy used to escape the stressor (C_E) is dependent on the extent of swimming in excess of normal, the incurred oxygen debt, and the duration of escape. Assuming the fish swims at maximum speed to escape the stressor (see Discussion for further discussion of this assumption), then:

$$C_E = A_T(\delta R_\infty + O_\infty) \tag{2}$$

where δ is duration of escape (seconds), R_∞ is the metabolic rate of fish swimming at maximum speed (watts), and O_∞ is the cost of repaying the maximum post-exercise oxygen debt (kJ). A_T adjusts for temperature using the Arrhenius function of absolute temperature T:

$$A_T = e^{-\left(\left[\frac{E_a}{K}\right]\left[\frac{1}{T} - \frac{1}{T_r}\right]\right)} \tag{3}$$

where E_a is activation energy (0.5 eV [Gillooly et al., 2006]), K is the Boltzmann constant ($8.62*10^{-5}$ eV/T), and T_r is an arbitrary reference temperature. For background and justification of Equations 3 and 5–8 see Sibly et al. (2013).

Injury or behavioural change due to exposure to the stressor will impact on energy uptake by reducing preference and/or ability to feed, causing changes to rate or quality of food acquisition, and a subsequent reduction in energy available for life processes. If Δ is the percentage loss in energy uptake due to injury or feeding impediment and E_i is the annual energy uptake by each fish, then:

$$C_I = \Delta E_i / 100 \tag{4}$$

We define the sublethal impact of the stressor as the percentage reduction in maximum annual rate of growth or reproduction caused by the stressor. This is achieved by modelling the allocation of energy to different vital processes (i.e. maintenance, growth and reproduction) and assessing the consequences for annual growth or reproduction relative to what can be achieved by a fish attaining maximum rates. After calculating the energy needed to cover maintenance, growth and reproduction (Equations 5–8), the allocation of energy between different processes is complex (Sibly et al., 2013). For simplicity, we take a worst-case approach, assuming the stressor acts solely on either growth or fecundity. So, when considering effects on growth, we assume fecundity has been prioritized and fecundity costs are the same as in unstressed fish. But when considering effects on fecundity, we assume growth is prioritized and growth costs are the same as in unstressed fish. This allows computation of maximum sublethal effects on growth or reproduction without introducing assumptions about how energy is partitioned among the processes.

Maximum rates of ingestion, maintenance, growth and fecundity all depend on the size of the fish (Sibly et al., 2013), taken here as size at the start of the year. The annual amount of energy that can be ingested each year (E_i) is as follows:

$$E_i = \alpha M^{\frac{2}{3}} E_f \sigma A_T \tag{5}$$

where α is the mean voluntary food ingestion (g/day $g^{-2/3}$), M is the mass of the fish (g), E_f is the energy content of one gram of food (J) and σ is the feeding season length. The energy ingested is used to fuel maintenance, growth and reproduction, but may be reduced by anthropogenic stressors.

The annual cost of maintenance (C_M) is as follows:

$$C_M = 2A_T S_a M^{0.79} \times 365 \tag{6}$$

where S_a is a normalizing constant and is calculated from standard metabolic rate (SMR) data from respirometer experiments and a scaling factor of 0.79 is applied to mass for marine fish (Peters, 1986). *FMR* is obtained from *SMR* by multiplying by two (Peters, 1986), and the daily cost is multiplied by 365 to give the annual cost of maintenance. When the cost of maintenance has been paid then any remaining energy assimilated is allocated to growth and/or reproduction.

The maximum annual cost of growth (C_{G_∞}, kJ y^{-1}) is as follows:

$$C_{G_\infty} = 3K_y A_T (M_\infty^{1/3} M^{2/3} - M) * 10.6 \tag{7}$$

where K_y is the annual growth constant and M_∞ is maximum mass. Growth is modelled using the von Bertalanffy equation and the annual energy cost of growth is calculated by multiplying maximum annual growth rate by the energetic cost of producing one gram of new flesh (10.6 kJg^{-1}; general value from Sibly et al., (2013).

The cost of producing a maximum amount of eggs for mature females ($C_{F\infty}$) is as follows:

$$C_{F\infty} = E_i - (C_{G_\infty} + C_M) \tag{8}$$

where we assume that all energy left over, after covering the cost of maintenance (C_M) and growth (C_{G_∞}), is available for fecundity.

2.2 | Application to C&R angling for European sea bass

To investigate the sublethal impact of C&R angling on sea bass, the model was parameterized using data from the literature (Table 1). To ascertain the energetic demands of sea bass, data were compiled from studies in respirometers (for details see Table 1). Respirometer experiments recorded oxygen consumption which we convert in to watts (assuming O^2 = 20 Jml^{-1} [Peters, 1986]), the rates of energy use are then corrected from the experimental temperatures (Table 1) to the model reference temperature using the Arrhenius function (Equation 3). Sea bass is reported to feed less avidly in water below 10°C (Pickett & Pawson, 1994) so, for simplicity in the model, we assume individuals only feed and grow when sea surface temperature (SST) is 10°C or above. For UK waters, this occurs for 213 days a year on average based on monthly SST from sites around the UK coastline from 1966 to 2012 (CEFAS, 2018) and the overall average SST for these days was 14°C. To show how the energy-budget approach can be applied to other locations, we ran the model with the same bass parameters but with the ability to feed all year round and a mean SST of 20°C, representing recreational fishing of European sea bass in the Mediterranean.

In our case study, the escape from the stressor is the period during which the fish attempts to escape from the fishing rod, which is termed a fish fight. Fight durations are not generally recorded by recreational sea bass anglers, but videos of fights are placed on YouTube (https://www.youtube.com). We watched all videos (n = 74) publicly available in November 2017 and recorded the duration of fight (10–289 s) and the fish length (15–75 cm), estimated by comparison with length of the angler's forearm. For our case study, we use a range of fight durations of 0–300 s and the previously described method using Equations 2–6 with the sea bass specific parameters (Table 1). It was not possible to distinguish from videos if the fish was fighting maximally for the whole fight duration, so we assume fighting for the total duration as a worst-case scenario.

3 | RESULTS

Our results are presented for the case of C&R angling for European sea bass parameterized as in Table 1. To assess the sublethal effects of angling, we calculated the losses in energy, growth and fecundity that arise from a fish's efforts while fighting and from reduction in energy ingestion while feeding as a result of disturbance including injury. Losses are shown relative to the baseline of energy assimilated by undisturbed fish which achieved maximum ingestion rate and had sufficient energy to fulfil maximum growth (juveniles and mature fish) and fecundity (mature fish only) (see Methods for calculation details).

TABLE 2 Sensitivities of energy, growth and fecundity loss of recreationally caught and released European sea bass to 10% changes in parameter values, presented as the % change in output averaged over an increase and decrease in the parameter value

	Energy		Growth		Fecundity	
Parameter	**Escape**	**Dist[c,a]**	**Escape**	**Dist[c,a]**	**Escape**	**Dist[c,a]**
Mean voluntary food ingestion (α)	10	10	0	7	49	59
Energy content of one gram of food (E_f)	10	10	0	67	49	59
Metabolic rate normalization (S_a)	–	–	0	0	49	42
Maximum mass (M_∞)	–	–	6	10	3	4
Feeding season length (σ)	10	10	0	0	49	62
Annual growth constant (K_y)	–	–	10	17	6	7

Note: Results are for a fish of middle size and a middle disturbance scenario (fish length = 42 cm, escape duration = 200 s and a disturbance of 50% reduction of feeding for 20 days, see Tables S1 and S2 for analyses of other cases).

[a] Disturbance.

TABLE 1 Parameter values used in Equations 2–6 (see methods for details) and experimental details of the studies from which values are obtained for the European sea bass catch and release fishing case study

Parameter	Value for sea bass	Reference	Experimental details
α Mean voluntary food ingestion	0.54 g/day $g^{-2/3}$	1	$N = 8$, L: $\mu = 37$, $R = 14$–34; M: $\mu = 1{,}023$, $R = 144$–$2{,}749$; Θ: $R = 6$–20
K_y Annual growth constant	0.09 $year^{-1}$	2	N/A
M_∞ Maximum mass	10 kg	3	N/A
S_a Metabolic rate normalization	0.12	4–8	$N = 7$, L: $\mu = 26$, $R = 14$–34; M: $\mu = 217$, $R = 26$–420; Θ: $R = 7$–20
φ Potential fecundity for mature female fish	0.3 × 106 eggs per kg of fish	9	N/A
E_e Energy to produce one gram of eggs	10.6 kJ	10	N/A
M_e Weight of one egg	0.96×10^{-3} g	11	N/A
E_f Energy content of one gram of food	3.5*0.5 kJ[a]	12	N/A
F_s Number of feeding days	213 days (UK)	3, 13	N/A
R_∞ Metabolic rate swimming at max speed	17.8–21.6 watts[b]	4, 5, 14–16	$N = 8$, L: $\mu = 37$, $R = 14$–34; M: $\mu = 1{,}023$, $R = 144$–2749; Θ: $R = 6$–20
SMR Standard metabolic rate	2.1–21.7 watts[b]	4–8	$N = 7$, L: $\mu = 26$, $R = 14$–34; M: $\mu = 217$, $R = 26$–420; Θ: $R = 7$–20
O_∞ Cost of repaying the max EPOC[c,a]	kJ	17	$N = 30$, L: $\mu = 32 \pm 1$, $R = 31$–35; M: $\mu = 520 \pm 64$, $R = 419$–643; Θ: $R = 11 \pm 0.5$°C
δ Duration of escape	10–289 s	18	$N = 74$ (videos available Nov/2017), L: $R = 15$–75 (estimated)

Notes: Experimental details; L = length (cm), M = mass (g), Θ = experimental temperature (°C), μ = mean, R = range. References: 1 = Lanari, D'Agaro, and Ballestrazzi (2002), 2 = Froese and Pauly (2018), 3 = Pickett and Pawson (1994), 4 = Claireaux (2006), 5 = Luna-Acosta, Lefrançois, Millot, Chatain, and Bégout (2011), 6 = Jourdan-Pineau, Dupont-Prinet, Claireaux, and McKenzie (2010), 7 = Zupa, Carbonara, Spedicato, and Lembo (2015), 8 = Peixoto et al. (2016), 9 = Pawson and Pickett (1987), 10 = Sibly et al. (2013), 11 = Cerdá, Carrillo, Zanuy, Ramos, and de la Higuera (1994), 12 = Peters (1983), 13 = CEFAS (2018), 14 = Wright, Metcalfe, Hetherington, and Wilson (2014), 15 = Herskin and Steffensen (1998), 16 = Chatelier, McKenzie, and Claireaux (2005), 17 = Ozolina, Shiels, Ollivier, and Claireaux (2016), 18 = YouTube videos.

[a] Assuming 50% of prey mass is flesh.

[b] Value range due to range of fish size.

[c] Excess post-exercise oxygen consumption.

3.1 | Local sensitivity analysis

The sensitivities of energy, growth and fecundity loss are shown in Table 2 as percentage change in output for a 10% change in the model parameters. These sensitivities are for medium-sized fish subject to intermediate levels of disturbance. Sensitivity differs between vital rates, the most sensitive parameters being associated with energy ingestion, which is expected as changes in energy inputs have direct effect on energy available for growth and reproduction. Sensitivities to 10% changes in the model parameters are generally less than or equal to 10% except for the sensitivity of fecundity loss, which is very high as a result of the way energy is allocated when calculating maximum rates: assimilated energy is allocated first to cover maintenance (C_M), and then growth (C_{G_∞}), only when these costs are paid is energy allocated to reproduction (Equations 7 and 8). To see how sensitivities vary with fish size and levels of disturbance, we ran the model with large mature fish (Length = 70 cm) and small immature fish (Length = 20 cm), in both severe (300 s fight, 45% reduction in feeding for 45 days) and minimal stress (30 s fight, 10% reduction in feeding for 10 days) scenarios (Tables S1 and S2). Fecundity losses were higher for large but lower for small fish compared with the values shown in Table 2 for medium fish. Conversely, growth losses were higher for small but lower for large fish compared with the values shown in Table 2 for medium fish. The severity of stress had generally little effect on small fish, but fecundity was negatively affected in large fish (Tables S1 and S2).

3.2 | Effects on energy, growth and fecundity loss

The effects of fight duration on energy, growth and fecundity losses are shown in Figure 1 in relation to fish length. Losses increase with fight duration, as expected, but the effects of fish length are more nuanced. The energy cost of fish fights as a percentage of total annual ingested energy is very small. Smaller fish that are involved in a longer fight experience the most severe energy loss, but this only equates to a maximum of 1% loss of annual energy (Figure 1a). Growth losses, shown in Figure 1b, are calculated for juvenile and mature sea bass; in the latter, we assume spawning occurs at its maximum rate. Growth losses are at most 3.5%, when a 60 cm fish is involved in a 300 s fish fight (Figure 1b). For immature fish, growth loss reduces as the fish grow, but then increases after maturity at 42 cm as the fish is then assumed to produce eggs at maximum rate, and larger fish become increasingly affected (Figure 1b). By contrast, fecundity losses vary very little with fish length (Figure 1c). The results in Figure 1 relate to the worst-case scenario that a fish caught by an angler attempts to escape by burst swimming. We assume the fish is swimming away at maximum speed for the whole fight (see Discussion for justification of this assumption), though in reality, a fish can only maintain maximum speed for a very short period due to physiological limitations (Horodysky et al., 2015).

After the initial fight, injury or behavioural change may affect ability or preference to feed as a result of physical damage from fishing gear and/or air exposure whilst being caught (Siepker, Ostrand, & Wahl, 2006). Losses in energy ingested, growth and fecundity are affected by both the duration and the level of reduction in feeding, as shown in Figures 2 and 3 for mature female and juvenile sea bass, respectively. Over the parameter ranges investigated, energy losses for mature bass could be as high as 60%, with consequent growth and fecundity losses up to 100% and 60%, respectively (Figure 2). Juvenile sea bass shows smaller energy and growth losses than adults, up to 30% and 50%, respectively (Figure 3). Scenarios resulting in larger/longer reductions in feeding have as expected greater losses of energy, growth and fecundity (Figures 2 and 3).

The effects shown above are for fish living in UK waters, which are assumed to be able to feed for 213 days a year when the sea surface temperature is assumed to be 14°C. Fish in other areas may experience different conditions, but their effects can be readily calculated using our energy-budget analysis. Although the individual rates of ingestion, maintenance and growth increase with temperature, the relative effects of escape and disturbance (those shown in Figures 1–3) would not change with temperature if the number of feeding days was kept constant. However, number of feed days is likely to increase with average temperature. Sea bass in the Mediterranean, for example, is able to feed year round. If we assume sea surface temperatures, there are 20°C and update the annual growth constant appropriate for Mediterranean temperatures ($K_y = 0.03$ [Froese & Pauly, 2018]), we find that all losses are reduced. Both growth and fecundity losses are less than in UK waters; fecundity losses 8% as opposed to 28% and growth losses 14% as opposed to 48%. These figures are for a particular scenario of a 50 cm sea bass fighting for 150 s and experiencing injury that reduces its ability

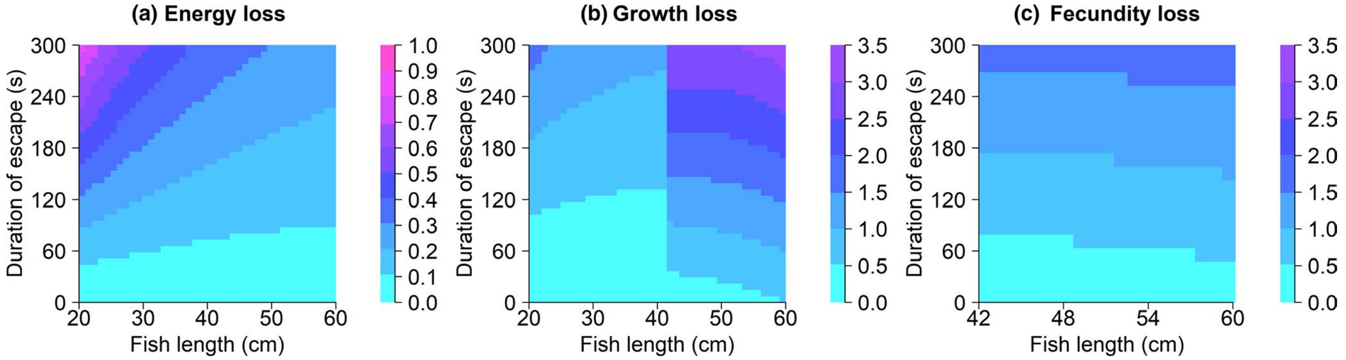


FIGURE 1 Effects of fish fights on growth and fecundity of recreationally caught and released European sea bass in relation to fish length and fight duration. Effects are shown as % loss of annual rates of (a) Ingested energy (b) growth and (c) fecundity, relative to fish achieving maximum growth or fecundity, respectively. The scale of % loss is shown on the right (figure appears in colour in the online version only)

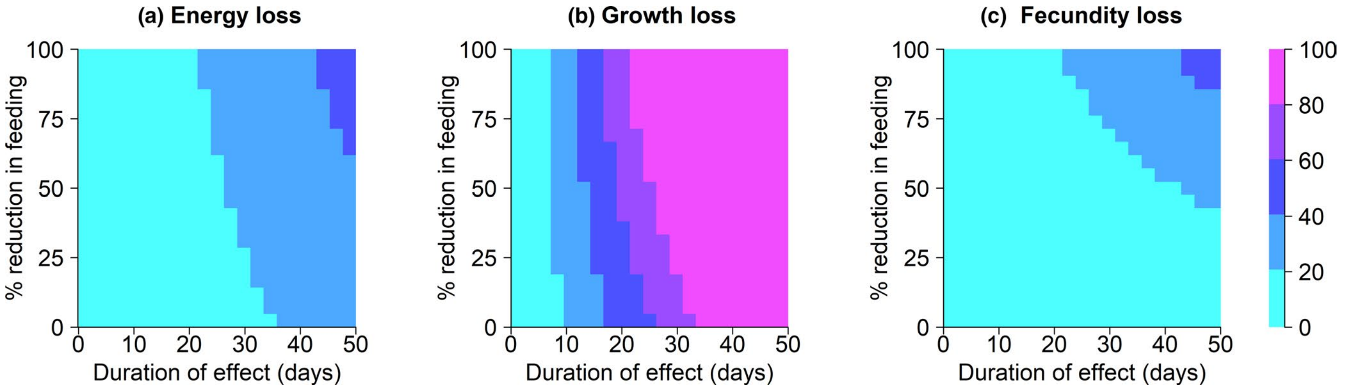
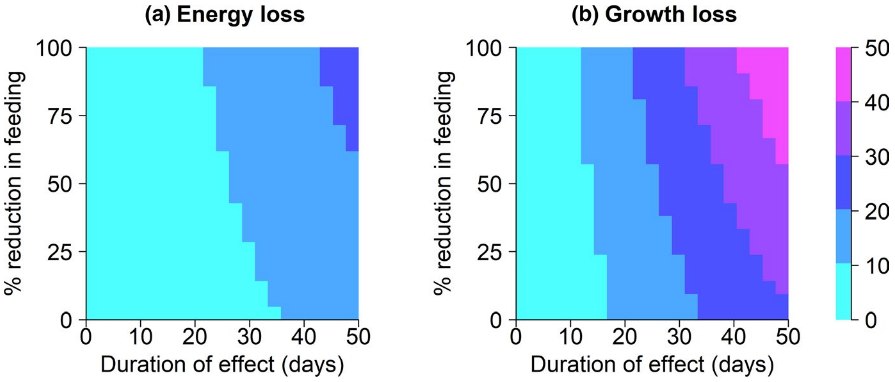


FIGURE 2 The effects of the duration and severity of capture/release effects, measured as % reduction in feeding, on energy intake, growth and fecundity of mature female European sea bass (42 cm). Effects are shown as % loss of annual rates of (a) Ingested energy, (b) growth and (c) fecundity, relative to fish achieving maximum energy intake, growth or fecundity, respectively. The scale of % loss is shown on the right (figure appears in colour in the online version only)

FIGURE 3 The effects of the duration and severity of capture/release effects on food intake, growth and fecundity of juvenile European sea bass (20 cm). Effects are shown as % loss of annual rates of (a) Ingested energy and (b) growth, relative to fish achieving maximum food intake and growth respectively. The scale of % loss is shown on the right (figure appears in colour in the online version only)



to feed by 50% for 20 days, but we expect that losses will generally be lower where feeding conditions are better.

4 | DISCUSSION

With increasing human populations, the impact of anthropogenic disturbances on the aquatic environment is growing (Vitousek et al., 1997). Stressors to fish such as anthropogenic noise (Slabbekoorn et al., 2010), fishing and pollutants (Kappel, 2005) can cause both lethal and sublethal impacts. The method introduced here uses energy budget models to investigate the often under-reported sublethal effects of stressors on growth, reproduction and ultimately fitness of fish. The models are not intended to replace existing experimental approaches, which are the method of choice, but to be used alongside when logistic constraints limit what can be achieved experimentally. For example, our method can be used as an initial step and can help identify needs for further analysis and experiments.

Unique to our method, over other bioenergetics stressor models (Beyers & Rice, 2002; Beyers et al., 1999; Beyers et al., 1999; Rice, 1990), is splitting the impact of the stressor into two parts. Firstly, assuming an escapable acute stressor, the fish may attempt to flee; this could include dodging an oil spill, avoiding anthropogenic noises or trying to break free from commercial or recreational fishing gear. The period for which fish swim to escape depends on many factors specific to individual stressors. For example, it may depend on the proximity of the fish to an oil spill, construction project or, in a fishing situation, how long gear is being pulled. In these situations, the fish is swimming at speed away from somewhere it does not want to be and is forced to spend energy that is subsequently unavailable for life processes. Some fish, however, freeze instead of attempting to escape, the metabolic implications of this would require similar analysis (Rupia, Binning, Roche, & Lu, 2016) but is not covered here. As well as escaping, the fish may suffer an injury or endure a change in behaviour due to the stressor. This could be an injury from commercial or recreational fishing gear (e.g. mouth damage from a hook), changed behaviour because of chemicals in the water, disturbance from marine construction or shipping noise. Such effects may impact an individual fish's ability and preference to feed, resulting in reduced ingested energy available for life processes. To show a broad range of possible impacts, we display our results on heat maps that allow the simultaneous display of many combinations of reduced ingestion rates and durations of effect (Figures 1–3). Each combination of these is unique and equates to a loss of energy. When this loss is compared with the energy needed to achieve life processes it is possible to investigate the impact of the stressor in question.

To demonstrate the method in practice, we chose as a case study the European sea bass subject to the stress of recreational C&R fishing in the UK. In our worked example, the initial escape is the fish fight attempting to escape from recreational fishing gear. We show how the combination of fight duration and the size of fish affect the energetic cost of the fight and the subsequent impact on growth and reproduction (Figure 1). As described in methods, our analysis is worst case: when considering effects on growth, we assume fecundity has been prioritized and fecundity costs are the same as in unstressed fish, but when considering effects on fecundity we assume growth is prioritized and growth costs are the same as in unstressed fish.

The initial energetic cost of the fish fight is very small when compared to annual ingested energy; however, this small amount of energy does show knock-on effects on both growth and fecundity (Figure 1). In immature bass (<42 cm), the pattern of growth loss mirrors that of energy loss and smaller immature bass are worse affected (Figure 1b). This pattern switches at maturity, and larger bass is then more affected, because they pay the same fecundity costs as unstressed fish. Fecundity costs are greater in larger fish, leaving less energy available to fuel growth.

After the initial fight, the released fish may suffer injury or changed behaviour due to the capture event. This is analysed in Figures 2 and 3 by looking at how injury or behavioural change can reduce ingestion and cause knock-on effects on growth and reproduction. Here, the patterns of loss of growth/reproduction reflect those of energy loss. Effects on growth are greater than those on reproduction, and Figure 2b shows that in extreme cases growth may cease altogether during the study year. Growth losses are more severe in adults than in immature fish (compare Figures 2b and 3b) because adults are assumed to pay fecundity costs. We show how the energy-budget approach can be used to assess the effects of changing location by applying it to the Mediterranean, where we predict smaller losses in the warmer Mediterranean temperatures. As expected physiologically, ingestion, metabolic and growth rates all increase in warmer waters, but the number of feeding days increases too. More feeding days result in more energy being ingested, and because losses are calculated per annum, the net effect of the warmer temperatures is that losses are reduced. The model could be used in a similar way to test inter-annual temperature fluctuations or climate change-driven sea temperature changes.

Our energy budget approach enables initial investigation of stressor effects on individual fish, but for many applications, it will be important to consider how a stressor affects entire fish populations (with a notable exception of animal welfare studies where the focus is on individuals [Cooke & Sneddon, 2007; Davie & Kopf, 2006]). In our case study, a population analysis would require data on numbers and size distribution of bass being caught. Currently, there are limited data on recreational fishing pressure, but relevant estimations may become possible as recreational fisheries become increasingly included in fisheries management (Radford et al., 2018). More broadly for anthropogenic stressors, Pirotta et al., (2018) suggest that one way to approach population impacts is using individual-based models (IBMs). IBMs use a bottom-up approach and simulate a population of discreet individuals where a combination of individual state and environmental variables change individual behaviour (DeAngelis & Grimm, 2014). In an IBM, each individual reacts to stressors uniquely depending on, among many other things, its energy reserves, life stage, size and proximity to the stressor. The proportion of individuals within a population that are affected and the severity of these impacts on their life process determine the population-level impacts of the stressor (Grimm & Railsback, 2005). The estimated effect of a stressor would be relevant in many cases of fisheries management. For example, stressor effects could change depending in/out spawning season, or they may impact size-at-age with potential knock-on effects on time to reach maturity and fecundity. An IBM could also be used to test food-limited scenarios (Boyd, Roy, Sibly, Thorpe, & Hyder, 2018) when even mild impacts of the stressor may impact on the ingestion rate enough to show previously unforeseen emergent population-level effects. Gordon et al. (2018) identify scenarios in which individual fish may simultaneously experience combination of stressors. The use of an appropriate IBM in combination with our energy budget approach could be used to quantify the population impacts of multiple stressors varying in time and space.

4.1 | Limitations and further research

Our method is broad and could, with appropriate consideration, be applied to a wide range of anthropogenic stressors and fish species. As in other bioenergetics models (e.g. Beyers & Rice, 2002), to apply this method to different stressors or species it is necessary to collect relevant values for duration of escape, if any, and re-parametrize Equations 2–8 for the intended species (Table 1). If the ultimate aim is a predictive model then validation must be given thought; here, we discuss some important considerations that would need to be addressed and some suggested experimental approaches that could provide validation data.

We are currently limited to investigating effects within one year and our method does not cover injuries or behaviour that extend beyond this. Within the current model, catch-up growth is not considered where some species may be able to make up lost growth after a stressor event (i.e. compensatory growth; see example with largemouth bass (*Micropterus salmoides*, *Centrarchidae*) in Cline, Weidel, Kitchell, & Hodgson, 2012. However, once embedded in a suitable IBM, lifetime effects, including compensatory growth, could be studied.

For escape duration, our analysis assumes fish are swimming away from the stressor at maximum speed for the entire duration of escape and we assume that they incur a maximal oxygen debt. In reality, there are physiological limitations which limit fish to short burst of maximum effort (Horodysky et al., 2015). Furthermore, for stressors that require fish to swim for long durations, this may be an excessive estimation of used energy, so ours is a worst-case, precautionary approach. One way to extend our precautionary approach and cover a non-escape response is to use burst swimming as an approximation of any increased metabolic rate due to the stressor stimuli. To better predict energetic costs and consequences beyond simple worst-case scenarios, would require detailed information on swimming behaviour during stressor escape and/or any other metabolic changes. Data for this could be from tagging experiments to measure how long and fast fish swim (Brownscombe et al., 2013; Graves, Horodysky, & Latour, 2009; Horodysky et al., 2015) and respirometer experiments for changes in metabolic rate (Rupia et al., 2016).

There are also aspects of injury and behavioural changes after escape that are not accounted for in our model. Firstly, it may be important to consider the disease status of the study species/stock, as infected fish may suffer additional complications from anthropogenic stressors. For example, striped bass in the USA that suffers from chronic diseases associated with *Mycobacterium spp*. (Gauthier et al., 2008) have been shown to suffer reduced reproductive success (Gervasi, Lowerre-Barbieri, Vogelbein, Gartland, & Latour, 2019), growth rates (Latour et al., 2012) and aerobic scope when exposed to hypoxic and warmer temperatures (Lapointe, Vogelbein, Fabrizio, Gauthier, & Brill, 2014). Furthermore, fish may suffer parasite or bacterial infections as a result of injuries or stress which could affect growth independently of feeding rate (Steeger, Grizzle, Weathers, & Newman, 1994). Account must also be taken of variation in fish life histories. For example, our model would underestimate the effect of disturbance on brood protecting species such as smallmouth and largemouth bass (*Micropterus dolomieu* and *Micropterus salmoides*) (Hanson, Cooke, Suski, & Philipp, 2007). When brood protecting species are subjected to C&R or other disturbances they are less able to defend their eggs (Pinder, Velterop, Cooke, & Britton, 2017; Suski, Svec, Ludden, Phelan, & Philipp, 2003), and the increased risk of brood predation leaves a reproductive sublethal impact on top of the energy lost during disturbance. Finally, fish species may differ in their stress responses, from complete inhibition to increase of reproduction (Hall, Broadhurst, Butcher, & Rowland, 2009; Lowerre-Barbieri, Vose, & Whittington, 2003; Schreck, Contreras-Sanchez, & Fitzpatrick, 2001). Such factors may vary the sublethal impacts of stress from those calculated using our exclusively energetics-based approach.

4.2 | Conclusions

We show a broadly applicable, complementary approach to field investigations that can be used to investigate sublethal impacts of a broad range of anthropogenic stressors on life processes of individual fish. Our approach builds on established bioenergetics approaches and provides a comprehensive energetics overview through from initial escape to longer-term injury/behavioural changes. We demonstrate its application to C&R fishing of European sea bass and show impacts ranging from zero to losses of up to 100% growth and 62% fecundity. Validation of the model is out of the scope of this study but we suggest experimental approaches that could be used to gain potential data and parameters and extend the model utility. We further suggest using IBMs to investigate combinations of anthropogenic stressors that vary over time and space for more detailed analysis of population-level effects. Our comprehensive energy budget approach, embedded within an IBM, could indicate emergent population-level effects for a broad range of anthropogenic stressors and cumulative impacts for many species and hence contribute to understanding and mitigating sublethal anthropogenic impacts on fish.

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CONFLICT OF INTEREST

No authors have conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created in this study.

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SUPPORTING INFORMATION

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

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